Chapter 3

Fisher

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INTRODUCTION

Natural History

The fisher (*Martes pennanti*) is a medium-size mammalian carnivore and the largest member of the genus *Martes* (Anderson 1970) of the family Mustelidae in the order Carnivora. The genus *Martes* includes five or six other extant species. The fisher has the general body build of a stocky weasel and is long, thin, and set low to the ground. A fisher's head is triangular with a pronounced muzzle, its ears are large but rounded, and its eyes face largely forward (Douglas and Strickland 1987). Adult male fishers generally weigh between 3.5 and 5.5 kg and are between 90 and 120 cm long. Adult female fishers weigh between 2.0 and 2.5 kg and are between 75 and 95 cm long. The weights of adult females are more constant than those of adult males over the species' range (Powell 1993).

From a distance fishers often look uniformly black but they are actually dark brown over much of their bodies. Guard hairs on a fisher's tail, rump, and legs are glossy black while those on the face, neck, and shoulders are brown with hoary gold or silver tips (Coulter 1966). The undersurface of a fisher is uniformly brown, except for white or cream patches on the chest and around the genitals. These patches might be used to identify individuals (Frost and Krohn, unpubl. data; Powell, unpubl. data).

The fur of fishers is very soft and glossy but varies among individuals, sexes, and seasons. Males have coarser coats than females. The single yearly molt may begin during late summer and is finished by November or December (Coulter 1966; Grinnell et al. 1937; Powell 1985, 1993). During September and October, the guard hairs are noticeably shorter than during the rest of the year, giving fishers a sleek appearance.

Fishers have five toes on all four feet. Their claws are retractable but not sheathed. Fishers are plantigrade and their feet are large. There are pads on each toe and four central pads, one each behind digits 1, 2 and 3, 4, and 5, on each foot. From the central pads to the heels of the hindpaws, there are coarse hairs covering tough skin. The small, circular patches of coarse hair on the central pads of the hindpaws are associated with plantar glands and carry an odor distinctly different from other fisher odors (Buskirk at al. 1986; Powell 1977, 1981a, 1993). Because these patches enlarge on both males and females during the breeding season (Frost and Krohn, unpubl. data), as they do in American martens (*Martes americana*; Buskirk et al. 1986), they are probably involved in communication for reproduction.

Fishers leave a characteristic mustelid track pattern: two footprints next to each other but slightly out of line. Deep, fluffy snow and thin crusts restrict fishers' movements (Grinnell et al. 1937; Heinemeyer 1993; Leonard 1980b, 1986; Powell 1977; Raine 1983) and, to avoid deep snow, fishers sometimes hunt in habitats in which they can travel most easily rather than in habitats that have most prey (Leonard 1980b; Raine 1983, 1987). Distribution of deep winter snow may limit fisher distribution (Aubry and Houston 1992; Krohn et al., in press) and may affect success of reintroductions (Heinemeyer 1993) and perhaps reproduction (Krohn et al., in press).

At the time of European settlement, fishers were found throughout the northern forests of North America and south along the Appalachian and Pacific Coast mountains (Graham and Graham 1994). The northern limit to the range is approximately 60°N

latitude west of Hudson Bay and the latitude of the southern tip of James Bay to the east. Between 1800 and 1940, fisher populations declined or were extirpated in most of the United States and in much of Canada due to overtrapping and habitat destruction by logging (Brander and Books 1973; Irvine et al. 1964; Powell 1993). Closed trapping seasons, habitat recovery programs, and reintroduction programs allowed fishers to return to some of their former range (Gibilisco 1994; Powell 1993). Populations have never returned to the Southern Appalachians, and populations are extremely low in Oregon and Washington (the Pacific Northwest) and parts of the northern Rocky Mountains (Aubry and Houston 1992; Gibilisco 1994; Powell 1993).

In eastern forests, fishers occur predominantly in dense lowland and spruce-fir habitats with high canopy closure (Arthur et al. 1989b; Kelly 1977; Powell, 1994b; Thomasma et al. 1991, 1994). Aside from avoiding areas with little cover (Powell 1993), fishers use most forest types within extensive northern-conifer forests (Buck et al. 1983; Coulter 1966; Hamilton and Cook 1955; Jones 1991; Raine 1983) and within mixed-conifer and northern-hardwood forests (Clem 1977; Coulter 1966; Johnson 1984; Kelly 1977; Powell, 1994b; Thomasma et al. 1991, 1994). These mustelids occur in extensive, mid-mature, second-growth forests in the Midwest and Northeast (Arthur et al. 1989b; Coulter 1966; Powell 1993) but have been considered obligate late-successional mammals in the Pacific Northwest (Allen 1983; Harris et al. 1982). Later authors (Ruggiero et al. 1991; Thomas et al. 1993) have categorized the species as "closely-associated" with late-successional forests. Buck et al. (1983), Seglund and Golightly (1994, unpubl.), and Jones (1991) considered riparian areas important for fishers in California and Idaho. Although Strickland et al. (1982) suggested that fishers could inhabit any forested area with a suitable prey base, the distribution of fishers does not include the extensive southern forests of the eastern United States or the extensive conifer and mixed-conifer forests of the Rockies south of Wyoming (Powell 1993). Buskirk and Powell (1994) hypothesized that tree species composition is less important to fishers than aspects of forest structure which affect prey abundance and vulnerability and provide denning and resting sites. Such forest structure can be characterized by a diversity of tree sizes and shapes; light gaps and associated understory vegetation; snags; fallen trees and limbs; and limbs close to the ground.

Because fishers are generalized predators, their major prey are small- to medium-sized mammals, birds, and carrion (reviewed by Powell 1993). Wherever abundant, snowshoe hares (*Lepus americana*) are common prey. Other common prey include squirrels (*Sciurus* sp., *Tamiasciurus* sp., *Glaucomys* sp.), mice (*Clethrionomys gapperi, Microtus* sp., *Peromyscus* sp.), and shrews (*Blarina* sp., *Sorex* sp.). The porcupine (*Erethizon dorsatum*) is the fisher's best known prey but does not occur in fishers' diets at some locations due to low population densities. Carrion is eaten readily and is mostly that of large mammals, such as deer (*Odocoileus* sp.) and moose (*Alces alces*). Seasonal changes in diet are minor and sexual differences have not been found (Clem 1977; Coulter 1966; Giuliano et al. 1989; Powell 1993).

Newborn fishers weigh 40-50 g and are completely helpless; their eyes and ears are tightly closed (Coulter 1966; Hodgson 1937; LaBarge et al. 1990; Leonard 1986; Powell 1993). When 2 weeks old, kits are covered with light silver-gray hair and by age 3 weeks, kits are brown. By 3.5 weeks of age, white ventral patches may be visible. Their eyes open when 7-8 weeks old and teeth erupt through the gums at about the same age. Kits are completely dependent on milk until 8-10 weeks old. They cannot walk well until 8 weeks of age or older but by 10-12 weeks of age can run with the typical mustelid gait. From ages 10-12 weeks through 5-6 months, young fishers are the same general color as adults but are more uniform in color. Sexual dimorphism in weight between males and females is first apparent around age 3 months and is pronounced by late autumn (Coulter 1966; Hodgson 1937; Powell 1993).

Aggression between fisher kits begins at about 3 months of age (Coulter 1966; Powell 1993) but kits cannot kill prey until about 4 months of age. They do not require parental instruction to learn proper killing techniques (Kelly 1977; Powell 1977). Kits remain within their mothers' territories into the winter (Powell, unpubl. data), but most juveniles have established their own home ranges by age 1 year (Arthur et al. 1993).

Current Management Status

Fisher populations are formally protected in four western and northwestern states in the United States: Oregon, Utah, Washington and Wyoming (table 1). California and Idaho have closed their trapping seasons; California has not had an open season since

Table 1.--Current management status of fishers in the western United States and Canada.

Jurisdiction	Length of trapping season (weeks)	Year fishers reintroduced
Alberta	0-15	1990
British Columbia	0-20	
Manitoba		1972-73[1]
Northwest Territories	19-21	
Saskatchewan	17	
Yukon	17	
California	0[2]	
Idaho	0[2]	1962-63
Montana	4-9	1959-60, 1988-91
Oregon	Protected	1961[1]
Washington	Protected	
Wyoming	Protected	

[1] Reintroduction failed.
[2] Fishers afforded protection through closed trapping season, but fishers are not afforded specific protected status.

1945. Montana has had an open trapping season since 1983-84 with a quota of 20 animals; all trapped fishers were to be reported and tagged (table 1). Concern has been expressed about the status of fisher populations in Washington, Oregon, and California (Central Sierra Audubon Society et al. 1990; Gibilisco 1994; USFWS 1991) and the fisher is a candidate for "threatened" status in Washington. The fisher is considered a sensitive species by the Forest Service in all Regions where it occurs, with the exception of Region 6 (Appendix C, table 4b).

All of the western provinces and territories of Canada have open fisher trapping seasons and Alberta and British Columbia require that all trapped fishers be reported and tagged (table 1). In Ontario, the ratio of the number of juvenile fishers harvested to the number of adult females harvested in a given year is used to project next year's relative population size and allowable harvest (Strickland 1994). This technique is empirical, however, and therefore may not be applicable to other fisher populations.

Fisher populations are found in second-growth forests from northern Ontario and Minnesota eastward. Available information from the West (Aubry and Houston 1992; Buck et. al 1994; Jones and Garton 1994), however, suggests that fishers are late-successional associates in that region. This difference may reflect a response to forest structure rather than seral stage (Buskirk and Powell 1994; Powell 1993). Krohn et al. (in press) have argued, however, that the distribution of deep snow may be an overriding influence on habitat use, even in areas with adequate prey populations. Fishers in different regions may have different ecologies. Until the habitat relationships of fishers have been adequately studied in the West, we should be cautious about applying the results of studies conducted in the East to the conservation of fishers in the West.

DISTRIBUTION AND TAXONOMY

Range

Although the genus *Martes* is Holarctic in distribution, fishers are found only in North America. Their present range is reduced from their range before European settlement of the continent (Gibilisco 1994; Graham and Graham 1994; Hagmeier 1956), but most of this reduction has occurred in the United States. During historical times the northern limit to the fisher's range has been approximately 60° N latitude in the west and somewhat south of the southern tip of James Bay in the east, following the 15.5° C isotherm. Once fishers ranged from what is now northern British Columbia into central California in the Pacific coastal mountains and south into Idaho, Montana and probably Wyoming in the Rocky Mountains. In the western mountains of the United States fishers have been reported in the following ecoprovinces (see Appendix A and B): Georgia-Puget Basin, Thompson-Okanogan Highlands, Columbia Plateau, Shining Mountains, Northern Rocky Mountain Forest, Snake River Basins, Pacific Northwest Coast and Mountains, Northern California Coast Ranges, and Sierra Nevada. Within this range fishers have occurred most commonly in northwestern California (the Northern California Coast Ranges Ecoprovince), the southern Sierra Nevada Ecoprovince, and in northern Idaho and northwestern Montana (the Shining Mountains and Northern Rocky Mountain Forest Ecoprovinces) (Appendix B).

In what is now the central United States, fishers may have ranged as far south as southern Illinois (Gibilisco 1994; Graham and Graham 1990, 1994; Hagmeier 1956). And in the eastern part of the continent, fishers ranged as far south as what is now North Carolina and Tennessee in the Appalachian Mountains (Gibilisco 1994; Graham and Graham 1994; Hagmeier 1956). Fisher remains from southern Illinois to Alabama are probably artifacts created by the trading and travel patterns of American Indians (Barkalow 1961; Graham and Graham 1990).

Historical Changes in Populations and Distribution

During the last part of the 19th century and the early part of this century, fisher populations declined strikingly. Fishers were extirpated over much of their former range in the United States and in much of eastern Canada (Bensen 1959; Brander and Books 1973; Coulter 1966; deVos 1951, 1952; Dodds and Martell 1971; Dodge 1977; Hall 1942; Ingram 1973; Rand 1944; Schorger 1942; Weckwerth and Wright 1968). Human activities, especially trapping and logging, contributed substantially to these declines. Both are capable of reducing fisher populations today and information available about the past decline is inconclusive as to whether one cause was more important than the other. In addition, trapping and logging are not independent because logging increases access to forests by trappers.

Fishers are known by trappers to be easy to trap (Young 1975) and prices paid for fisher pelts, especially the silky, glossy pelts of females, have always been high. Before the 1920's, there were no trapping regulations for fishers and high fur prices provided trappers with strong incentive to trap fishers (Balser 1960; Brander and Books 1973; Hamilton and Cook 1955; Irvine et al. 1964; Petersen et al. 1977). Prices have never been stable, however, and have not been the same throughout the United States and Canada. Peak prices were paid for fisher pelts in 1920 and in the 1970's and 1980's; lowest prices were paid in the 1950's and 1960's (Douglas and Strickland 1987; Obbard 1987).

The decrease in fisher populations began first in the East, undoubtedly because of the longer history of European settlement. New York fisher populations had already begun to decrease by 1850 (Hamilton and Cook 1955), but the decrease in Wisconsin was not great before the first part of this century (Schorger 1942; Scott 1939). Wisconsin closed its fisher trapping season in 1921 but by 1932 the fisher was believed extinct in Wisconsin (Hine 1975). Fisher populations persisted in California, Oregon, and Washington (Aubry and Houston 1992; Schempf and White 1977; Yocum and McCollum 1973) but the last reliable reports of native fishers in Montana and Idaho came during the 1920's (Dodge 1977; Weckwerth and Wright 1968). Because of warnings from biologists, other states followed the example set by Wisconsin and closed their fisher-trapping seasons.

Fisher populations in Canada also showed significant declines but the declines were somewhat obscured by pronounced 10-year population cycles in response to cycles in snowshoe hare populations. The numbers of fishers trapped throughout the country declined by approximately 40% between 1920 and 1940 (deVos 1952; Rand 1944). Between 1920 and 1950 the number of fishers trapped in Ontario declined by 75%, adjusted to the phases of the 10-year population cycle (deVos 1952; Rand 1944). Fishers were completely exterminated from Nova Scotia before 1922 (Bensen 1959; Dodds and Martell 1971; Rand 1944).

At the same time that fishers were heavily trapped, their habitat was being destroyed. By the mid-19th century, clearing of forests by loggers and farmers and by frequent forest fires reduced the forested area of much of the northeastern United States to approximately 50%, from 95% 200 years earlier (Brander and Books 1973; Hamilton and Cook 1955; Silver 1957; Wood 1977). Land clearing in the Upper Midwest occurred during the early 20th century (Brander and Books 1973; Irvine et al. 1962, 1964). Either trapping or habitat destruction by itself could have dramatically reduced fisher populations; together, their effect was extreme. During the 1930's, remnant fisher populations in the United States could be found only on the Moosehead Plateau of Maine, in the White Mountains in New Hampshire, in the Adirondack Mountains in New York, in the "Big Bog" area of Minnesota, and in the Pacific States (Brander and Books 1973; Coulter 1966; Ingram 1973; Schorger 1942). In eastern Canada, the only remnant population was on the Cumberland Plateau in New Brunswick (Coulter 1966).

Concurrent with the closure of trapping seasons during the 1930's, the logging boom came to an end in eastern North America and abandoned farmland began to return to forest. The few remnant fisher populations in these areas recovered (Balser and Longley 1966; Brander and Books 1973). By 1949, wildlife managers in New York felt that the fisher population in that state had recovered sufficiently to reopen a trapping season. Over the following decades, trapping seasons were reinitiated in several states and provinces.

Following the reduction in fisher populations, porcupine populations climbed to extremely high densities in much of the forested lands in the United States (Cook and Hamilton 1957; Earle 1978). Porcupines were blamed for much timber damage (Cook and Hamilton 1957; Curtis 1944), though the damage was often exaggerated (Earle 1978). It is difficult to quantify the damage caused by porcupines be-

cause porcupines also beneficially prune trees (Curtis 1941). Nonetheless, damage did occur in areas with very high porcupine populations (Krefting et al. 1962). During the 1950's, interest in reestablishing fisher populations began to increase. Concurrent declines in the porcupine populations were noted in those areas of Minnesota, Maine, and New York where fisher populations were increasing (Balser 1960; Coulter 1966; Hamilton and Cook 1955). Cook and Hamilton (1957) suggested using fishers as a biological control for extremely high porcupine populations. Coulter (1966) warned, however, that there was no evidence that fishers could limit porcupine populations for long periods of time.

Nonetheless, during the late 1950's and 1960's, many states and provinces reintroduced fishers (table 1, Powell 1993). The purpose of these reintroductions was twofold: to reestablish a native mammal and to reduce high porcupine population densities (Irvine et al. 1962, 1964). Some states or provinces moved fishers within their borders, others released fishers from other jurisdictions. Not all releases succeeded in reestablishing fisher populations, but many did. A few states, for example Vermont and Montana, augmented low fisher populations. Massachusetts and Connecticut have reestablished fisher populations largely through population expansion from other states. And fishers have occasionally been sighted in Wyoming, North Dakota, South Dakota, and Maryland.

Thus, the range of the fisher in eastern North America has recovered much of the area lost during the first part of this century. The fisher is again living in areas from northern British Columbia to Idaho and Montana in the West, from northeastern Minnesota to Upper Michigan and northern Wisconsin in the Midwest, and in the Appalachian Mountains of New York and throughout most of the forested regions of the Northeast (Balser 1960; Banci 1989; Berg 1982; Bradle 1957; Coulter 1966; Earle 1978; Gibilisco 1994; Heinemeyer 1993; Irvine et al. 1962, 1964; Kebbe 1961; Kelly 1977; Kelsey 1977; Morse 1961; Penrod 1976; Petersen et al. 1977; Powell 1976, 1977a; Roy 1991; Weckwerth and Wright 1968; Williams 1962; Wood 1977). Many states and provinces have trapping seasons for fishers and regulations are adjusted in an attempt to maintain fisher populations at current levels.

In the 1980's and early 1990's, trapping mortality in southcentral Maine exceeded reproduction (Arthur et al. 1989a; Paragi 1990). Fishers have not returned to the southern Appalachians. Illinois, Indiana, and Ohio may never again have forested areas extensive enough to support fisher populations. And in areas where there has been extensive, recent logging that fragments forests extensively, fisher populations have not recovered, perhaps because fishers appear sensitive to forest fragmentation (Rosenberg and Raphael 1986). There were only 89 potential sightings of fishers in Washington between 1955 and 1993 and only 3 were supported with solid evidence, such as photographs or carcasses. Fishers may be on the verge of extinction in Washington (Aubry and Houston 1992; Aubry, unpubl. records). Although no evaluation of their status and distribution in Oregon has been conducted, sightings are extremely rare (Appendix B; Aubry, unpubl. data). Recent work with remote cameras, however, has detected the presence of fishers just west of the Cascade Crest in southern Oregon (S. Armentrout, pers. comm.). Finally, the fisher population in the southern Sierra Nevada Mountains in California (Appendix B) may be doing well, but it appears to be isolated from the population in northwestern California (W. Zielinski, pers. obs.). The latter population has remained stable since the early part of this century (Grinnell et al. 1937; Schempf and White 1977) and may have the highest abundance of all populations in the western United States.

It is sometimes necessary to augment isolated fisher populations with fishers captured elsewhere. Fishers have been released in eastern North America to reestablish populations where fishers had gone extinct. Releases have generally been unsuccessful in western North America. Roy's (1991) results indicate that many fishers from eastern North America may lack behaviors, and perhaps genetic background, to survive in western ecological settings. If fishers are moved from one population to another, inappropriate genetic background or ecotypic adaptations could have adverse effects on resident populations.

Irvine et al. (1962, 1964) recommended winter reintroductions. It has been believed, incorrectly, that females would not travel far as parturition approached (Roy 1991). Fishers reintroduced during winter travel long distances (Proulx et al. 1994; Roy 1991), however, and may be subject to greater risk of predation (Roy 1991) than they were in their capture sites.

Only once have fishers not been released during winter. Proulx et al. (1994) released fishers in the parklands of Alberta during both late-winter and summer. Fishers released during winter travelled significantly longer distances and had significantly higher mortality than the fishers released during

summer. Most fishers released in summer established home ranges close to their release sites, whereas this was not the case for the fishers released during winter. Proulx et al. recommended more experiments to find optimal release times; in the mean time, summer should be tried when possible.

Taxonomy

Goldman (1935) recognized three subspecies of fishers: *Martes pennanti pennanti, M. p. pacifica,* and *M. p. columbiana.* Recognition of subspecies, however, may not be valid. Goldman stated that the subspecies were difficult to distinguish, and Hagmeier (1959) concluded from an extensive study that recognition of subspecies was not warranted because the subspecies were not separable on the basis of pelage or skull characteristics. The continuous range of fishers across North America, allowing free interchange of genes, is consistent with a lack of valid subspecies. Anderson (1994) and Hall (1981) retained all three subspecies but failed to address Hagmeier's conclusion. On the basis of Whitaker's (1970) evaluation of the subspecies concept, Hagmeier was probably correct, but genetic analyses will be required to resolve this question.

Management Considerations

1. Isolated populations are of special concern and must be monitored.
2. Forest fragmentation may result in the isolation of populations.
3. Reintroductions would be most likely to succeed if translocated animals are from similar habitats in the same ecoprovince (Appendix A).

Research Needs

1. Develop, refine, and standardize survey methods to document the distribution of fishers in western North America.
2. Investigate the dispersal capabilities of fishers and characterize habitats and geographic features that facilitate or inhibit their movements, i.e., corridors and barriers.
3. Document genetic diversity within and among fisher populations to reevaluate named subspecies of fisher, to identify isolated populations that may require special management, and to identify similar genetic stocks for reintroduction.

4. Investigate factors that contribute to successful reintroductions and augmentations.

POPULATION ECOLOGY

Population Densities and Growth

Fisher population densities vary with habitat and prey, and density estimates in the northeastern United States have ranged from 1 fisher per 2.6 km^2 to 1 fisher per 20.0 km^2 (Arthur et al. 1989a; Coulter 1966; Kelly 1977). Coulter (1966) and Kelly (1977) did not believe that fishers could sustain densities of 1 fisher per 2-1/2-4 km^2 and Kelly reported a decrease in the number of fishers in New Hampshire and Maine following a period with such densities. Arthur et al. (1989a) calculated a summer density of 1 fisher per 2.8 to 10.5 km^2 in Maine and a winter density of 1 fisher per 8.3 to 20.0 km^2. The densities reported by Arthur et al. are the best available from the Northeast; they include seasonal changes in density caused by the spring birth pulse and they give the ranges of densities possible, showing the uncertainty of their estimates.

Information on fisher densities outside the Northeast is limited. Buck et al. (1983) estimated a density of 1 fisher per 3.2 per km^2 for their northern California study area. Fisher population densities in northern Wisconsin and Upper Peninsula Michigan have been estimated at 1 fisher per 12-19 km^2. (Earle 1978; Johnson 1984; Petersen et al. 1977; Powell 1977).

The density estimates for fisher populations vary for many reasons. Fisher populations fluctuate with populations of prey and in some places exhibit 10-year cycles in densities (Bulmer 1974, 1975; deVos 1952; Rand 1944) in response to 10-year cycles in snowshoe hare population densities (Bulmer 1974, 1975). Where fishers were reintroduced (e.g., Michigan, Wisconsin, Idaho, Montana), population densities may be low because of insufficient time for populations to build. Trapping in New England has at times been intense, even recently (Krohn et al. 1994; Wood 1977; Young 1975), and overtrapping can reduce populations in local areas (Kelly 1977; Krohn and Elowe 1993). Finally, it is difficult to estimate fisher population sizes because fishers do not behave according to the assumptions necessary to use most methods of estimating populations (e.g., equal trapability, no learned trap response, sufficient trapability to give adequate sample sizes). Therefore all estimates incorporate considerable sampling error.

W. Krohn (pers. comm.) suspects that as fishers colonize new, suitable habitat in Maine their density is initially very low, then rises to levels that probably cannot be maintained, and finally falls to intermediate levels. This pattern is consistent with information available from Wisconsin as well (C. Pils, pers. comm.). It is the pattern of population growth expected for animals whose density-dependent feedback comes through changes in adult and juvenile mortality rather than through changes in reproduction. Such a pattern is consistent with changes in fisher population density that track cycles in snowshoe hare numbers (Bulmer 1974).

This pattern of rapid population increase has not been observed in western populations, many of which have failed to recover despite decades of protection from trapping (e.g., northern Sierra Nevada, Olympic Peninsula), reintroductions (e.g., Oregon), or both. Therefore, one or more major life requisites must be missing. Suitable habitat may be limited, colonization of suitable habitat may be limited due to habitat fragmentation, or some other factor or combination of factors may be involved. Other populations, most notably the one in northwestern California (R. Golightly, pers. comm.; W. Zielinski, pers. obs.), have sustained themselves while nearby populations have apparently declined and failed to recover.

York and Fuller (in press) summarized the life history information available for wild and captive fishers (all of which came from eastern populations). Using a simple accounting model, they estimated the exponential rates of increase for a number of hypothetical populations. Initial values for survival and reproductive parameters were set at the lowest, weighted mean, unweighted mean, and highest values for each of four runs. Only the model run that incorporated the highest values of survival and reproduction resulted in lambda values that exceeded 1.0. The authors interpreted this to mean that most fisher populations require immigrants to increase and that only those with high reproductive and survival rates are self-sustaining.

Survivorship and Mortality

Fishers have lived past ten years of age (Arthur et al. 1992), which may be near the upper limit of life expectancy (Powell 1993). They exhibit low incidence of diseases and parasites (Powell 1993). Few natural causes of fisher mortality are known. Fishers have choked on food (Krohn et al. 1994) and have been debilitated by porcupine quills (Coulter 1966; deVos 1952; Hamilton and Cook 1955). Healthy adult fishers appear not to be subject to predation, except fishers that have been translocated. A fisher in Maine was trapped on the ice and killed by coyotes (*Canis latrans,* Krohn et al. 1994) and a fisher was killed by a dog (*Canis familiaris*) in Ontario (Douglas and Strickland 1987). An adult female fisher in northern California was killed by a large raptor, probably a golden eagle (*Aquila chrysaetos*) or great horned owl (*Bubo virginianus,* Buck et al. 1983). Reintroduction of fishers to the Cabinet Mountains of Montana was hindered by predation; of 32 fishers from Wisconsin released in the Cabinet Mountains, at least 9 were killed by other predators (Roy 1991). All appeared to have been in good health. It is possible that the differences between Wisconsin and Montana in habitat, topography, prey, and predators somehow made these fishers vulnerable to predation.

Trapping has been one of the two most important factors influencing fisher populations. Management of fisher populations, either to stabilize populations and harvests (Strickland 1994) or to provide recreational harvests, replaces natural population fluctuations with fluctuations caused by periods of overtrapping followed by recovery when trapping pressure decreases (Berg and Kuehn 1994; Douglas and Strickland 1987; Kelly 1977; Krohn et al. 1994; Parson 1980; Wood 1977; Young 1975; reviewed by Powell 1993). This occurs despite adjustments in trapping regulations. Fishers are also easily trapped in sets for other furbearers (Coulter 1966; Douglas and Strickland 1987; Young 1975). Where fishers are scarce, the populations can be seriously affected by fox (*Vulpes vulpes, Urocyon cinereoargenteus*) and bobcat (*Lynx rufus*) trapping (Coulter 1966; Douglas and Strickland 1987). Whether population fluctuations caused by trapping affect social structure of fisher populations in the same manner as natural population cycles is not known.

Mathematical models for the fisher community in Michigan (Powell 1979b) indicated that small increases in mortality due to trapping could lead to population extinction. Depending on the model, the increase in mortality needed to lead to extinction was as low as 3% or as high as 98%. This is equivalent to an increase in mortality of 1-4 fishers/km^2 above natural mortality levels. These models did not incorporate sex or age structure in the model fisher populations.

Based on data from radio-collared fishers, Krohn et al. (1994) estimated mean annual mortality rates

over a five-year period from a population in Maine where 94% of all mortality was from commercial trapping. The sexes did not show significant differences in survivorship for either adults or juveniles outside the trapping season, but adult females had significantly higher survivorship than adult males during the trapping season. It is not known whether the sexes have similar survivorships in populations that are not harvested. Survivorship during the trapping season for adult females, adult males, juvenile females, and juvenile males was 0.79, 0.57, 0.34, and 0.39, respectively. During the non-trapping season, survivorship rates were 0.87, 0.89, 0.75, and 0.71. Using a model that incorporated differential susceptibility to trapping for fishers of different ages and sex, Paragi (1990) found that annual fall recruitment needed to maintain a stable population was approximately 1.5 offspring per adult female (≥2 years old). Actual recruitment was 1.3 offspring per adult female, indicating a 2% per year population decline.

Age Structure and Sex Ratio

Age-specific survivorships for fisher populations appear to fluctuate with prey populations. During periods of high prey availability, juvenile fishers comprise a higher-than-average proportion of a trapped population; when prey populations are low and fisher populations decline, cohorts of old fishers comprise higher-than-average proportions of the population (Douglas and Strickland 1987; Powell 1994a). Harvested populations of *Martes* species tend to be biased more toward young animals, on the average, compared to unharvested populations (Powell 1994a). Average age structure for the heavily trapped fisher population in Ontario is highly skewed toward young animals (Douglas and Strickland 1987).

Our understanding of age structure in fishers and other animals is hampered by biases in population biology and demography research, which have historically been oriented to understand population stability (e.g., Lomnicki 1978, 1988; May 1973). Unstable age structure leads to variations in population responses to changes in prey populations. Because fishers do not reproduce until age two, populations biased toward young animals may not be able to respond to increases in prey populations as rapidly as populations biased toward old individuals. Thus, trapping may affect the abilities of fisher populations to respond to increasing prey populations (Powell 1994a). Natural fisher populations may be character-

ized by episodes of local extinction and recolonization (Powell 1993), which we have hypothesized to be the norm for weasel populations (*Mustela frenata, M. erminea, M. nivalis* [= *rixosa*]; Powell and Zielinski 1983). If remnant populations in the Pacific Northwest and Rocky Mountains are reduced in number and sufficiently separated they may not be capable of recolonizing depopulated areas.

Sex ratios of unharvested fisher populations are poorly known and true sex ratios (primary, secondary, or tertiary) are difficult to determine. Live-trapping and kill-trapping results for all mustelines exhibit a significant bias toward males (Buskirk and Lindstedt 1989; King 1975). Sex ratios for natural fisher populations should be close to 50:50 (Powell 1993, 1994b). This trapping bias toward males might skew harvested populations toward females (Krohn et al. 1994; Powell 1994b). This will not, however, necessarily increase reproductive output of the population. The density of adult males must be sufficient for maximal reproduction and recruitment must exceed mortality.

Management Considerations

1. The reproductive rates of fishers are low, relative to other mammals, and low density fisher populations will recover slowly.

2. Population densities of fishers are low, relative to other mammals, and can undergo fluctuations that are related to their prey. These fluctuations make small or isolated populations particularly prone to extirpation.

3. Fishers are easily trapped and can frequently be caught in sets for bobcats, foxes, coyotes, and other furbearers. To protect fisher populations, trapping using land sets may need to be prohibited. Incidental trapping of fishers in sets for other predators may slow or negate population responses to habitat improvement.

Research Needs

1. Obtain demographic data (age structure, sex ratio, vital rates) for representative, untrapped populations in ecoprovinces in the West.

2. Develop methods of estimating fisher densities.

3. Use demographic data and density estimates to develop models to estimate viable population sizes.

REPRODUCTIVE BIOLOGY

Reproductive rates

The reproductive biology of female fishers is similar to that of other members of the Mustelinae (weasels, martens, and sables) (Mead 1994). Female fishers are sexually mature and breed for the first time at 1 year of age (Douglas and Strickland 1987; Eadie and Hamilton 1958; Hall 1942; Wright and Coulter 1967). Ovulation is presumed to be induced by copulation and the corpora lutea of actively pregnant female fishers can be readily identified (Douglas and Strickland 1987; Eadie and Hamilton 1958; Wright and Coulter 1967). Implantation is delayed approximately ten months, and, therefore, female fishers can produce their first litters at age two. Females breed again approximately a week following parturition. Pregnancy rates for fishers are generally calculated as the proportion of adult females (≥2 yr) harvested whose ovaries contain corpora lutea (Crowley et al. 1990; Douglas and Strickland 1987; Shea et al. 1985). Corpora lutea generally indicate ovulation rates of ≥95% (Douglas and Strickland 1987; Shea et al. 1985), while placental scars indicate much lower birth rates.

Far fewer than 95% of female fishers ≥2 years old den and produce kits each spring. From 1984 to 1989, 12 radio-collared female fishers in Maine had a denning rate of only 63% (Arthur and Krohn 1991; Paragi 1990). Fifty percent (3 of 6) of the adult females in Massachusetts produced litters (York and Fuller, in press). Although an average of 97% of the female fishers from Maine, New Hampshire, Ontario and Vermont had corpora lutea (range 92 to 100), only 58% had placental scars (range 22-88; Crowley et al. 1990). This indicates that placental scars document birth of kits better than do corpora lutea (Crowley et al. 1990). A controlled study in Maine, however, is currently investigating the retention of placental scars in captive female fishers known to have produced litters (Frost and W. Krohn, pers. comm.). Why some females that have bred fail to produce litters is unknown, but nutritional deficiency related to stressful snow conditions is suspected because reproductive indices are higher in areas of low snowfall (Krohn et al., in press). Estimates of average numbers of corpora lutea, unimplanted blastocysts, implanted embryos, placental scars, and kits in a litter range from 2.7 to 3.9 (reviewed by Powell 1993). York and Fuller (in press) summarized the mean litter sizes for fishers from seven studies and discovered that they ranged from 2.00 to 2.90. Paragi (1990) estimated survival rates from six weeks until late October for kits in Maine to be ≥0.6 and estimated fall recruitment at 0.7-1.3 kits/adult female.

Although it is usually assumed that sufficient numbers of males exist to breed with receptive females, this may not always be the case. Strickland and Douglas (1978; Douglas and Strickland 1987) found that trapping during January and February causes disproportionately high mortality of adult males, may decrease their numbers below that necessary to inseminate all females, and may even lead to population decline. In 1975 the fisher trapping season in the Algonquin region of Ontario was restricted to end on 31 December, reducing the trapping pressure on adult males. Thereafter, both the breeding rate of females and the population increased.

Breeding Season and Parturition

From mid-March through April, all adult males appear fully sexually active. Testes of fishers have been found with sperm as late as May (M. D. Carlos, Minn. Zool. Soc., unpubl. records; Wright and Coulter 1967). Despite having sperm, 1-year-old male fishers appear not to be effective breeders, probably because baculum development is incomplete. Beginning in March, adult male fishers, but not necessarily adult females, increase their movement rates and distances traveled (Arthur et al. 1989a; Coulter 1966; Kelly 1977; Leonard 1980b, 1986; Roy 1991). Established spacing patterns of adult males break down, they trespass onto the territories of other males, and they may fight (Arthur et al. 1989a; Leonard 1986). The first visible sign of estrus in female fishers is the enlargement of the vulva (Laberee 1941; Mead 1994) and females are in estrus for about 6-8 days (Laberee claimed only two days), beginning 3-9 days following parturition for adult females (Hall 1942; Hodgson 1937; Laberee 1941). Douglas and Strickland (1987) summarized the breeding season for fishers to be from 27 February to 15 April, based on known birth dates of captive litters, but this ignored the 3-9 day delay between parturition and breeding. Implantation can occur as early as January and as late as early April (Coulter 1966; Hall 1942; Hodgson 1937; Laberee 1941; Leonard 1980b, 1986; Paragi 1990; Powell 1977; Wright and Coulter 1967).

Parturition dates as early as February and as late as May have been recorded (Coulter 1966; Douglas 1943; Hall 1942; Hamilton and Cook 1955; Hodgson

1937; Kline and D. Carlos, Minn. Zool. Soc., unpubl. records; Laberee 1941; Leonard 1980b; Paragi 1990; Powell 1977; Wright and Coulter 1967). The only data from western North America are from fur farms in British Columbia, where parturition occurred during late March and early April (Hall 1942). Females probably breed within 10 days after giving birth. Thus, an adult female fisher is pregnant almost all the time, except for a brief period following parturition. Healthy females breed for the first time when they are 1 year old, produce their first litters when they are 2 years old, and probably breed every year thereafter as long as they are healthy.

Den Sites

Female fishers raise their young in protected den sites with no help from males. Almost all known natal dens (where parturition occurs) and maternal dens (other dens where kits are raised) have been discovered in eastern North America (Arthur 1987; Paragi 1990). Of these, the vast majority were located high in cavities in living or dead trees. This strongly suggests that female fishers are highly selective of habitat for natal and maternal den sites. Information is available for only two natal dens (California, Buck et al. 1983; Montana, Roy 1991) and one maternal den (California, Schmidt et al. 1993, unpubl.) in the western United States. The den found in Montana was in a hollow log 11 m long with a convoluted cavity averaging 30 cm in diameter. A natal den in California was in a 89 cm dbh ponderosa pine (*Pinus ponderosa*) snag. The maternal den was located in a hollow white fir (*Abies concolor*) log that was 1.5 m in diameter at the den site (Schmidt et al. 1993, unpubl.). Of the 32 natal dens found by Arthur (1987) and Paragi (1990) in Maine, over 90% were in hardwoods and over half were in aspens (*Populus* spp.). The den site Leonard (1980a, 1986) studied in Manitoba was also in an aspen. Because female fishers in eastern North America and in the Rocky Mountains are highly selective of habitat for resting sites (Arthur et al. 1989b; Jones and Garton 1994; Kelly 1977; Powell 1994b), they are probably highly selective of habitat for natal and maternal den sites as well.

Female fishers will use 1-3 dens per litter and are more likely to move litters if disturbed (Paragi 1990). The natal den found by Leonard (1980a, 1986) had no nesting material and was extremely neat after the kits left: no excrement, no regurgitated food, and no food remains. Natal nests of captive fishers are similarly spartan (Hodgson 1937; Powell, unpubl. data). A natal den found by Roy (1991), however, contained a dense mat of dried pine needles and moss. Roy also found a pile of 40-50 scats separated from the nest by 20 cm and behind a block in the cavity in the den log.

Except during mating, female fishers raised on fur farms spend little time outside natal nest boxes after parturition (Hodgson 1937; Laberee 1941). Although mating may keep a female away from her young for several hours when the young are only a few days old, she returns quickly to her young when she has finished mating. Wild female fishers exhibit individual variation in activity patterns both before and after weaning their kits. A female followed by Leonard (1980a, 1986) spent very little time away from her kits at first but spent increasingly more time away as they grew. Females followed by Paragi (1990) exhibited no discernable pattern. Kits are often moved from natal to maternal dens at 8 to 10 weeks of age (Leonard 1980b; Paragi 1990).

Scent Marking

During March fishers scent mark with urine, feces, musk, and black, tar-like marks on elevated objects such as stumps, logs and rocks (Leonard 1980b, 1986; Powell 1977). This March surge in scent marking coincides with the beginning of the breeding season as does the elaboration of plantar glands on the feet (Buskirk et al. 1986; W. Krohn, pers. obs.; Powell 1977, 1981a, 1993).

Fishers possess anal glands, or sacs, containing substances that have neither the strong nor offensive odor of weasels and skunks. The precise function of anal gland secretions is unknown. An odor and probably some secretion is discharged when wild fishers are frightened, such as when they are handled by humans (Powell 1993). In other mustelines, the anal gland secretions differ between males and females and change seasonally (Crump 1980a, 1980b). It is presumed that the anal gland secretions of fishers provide information to other fishers regarding sex, sexual activity, and perhaps maturity and territorial behavior.

Fishers lack abdominal glands (Hall 1926; Pittaway 1984), which are found in some but not all other *Martes* (de Monte and Roeder 1990; Rozhnov 1991). Other *Martes* have many glands on their cheeks, necks, and flanks (de Monte and Roeder 1990; Petskoi and Kolpovskii 1970). Fishers rub these areas, indicating that they may have glands there as well (R. Powell, pers. obs.).

Management Considerations

1. The recovery of fisher populations will be slow because fishers have small litters and do not produce their first litters until two year of age. Reproductive output of populations biased toward young fishers is limited by the inability of yearling males to breed effectively. Over-trapping may also bias the population toward young animals, further delaying recovery.

2. All natal and maternal dens in the West were found in large diameter logs or snags. These habitat elements may be reduced in stands that have been intensively managed for timber.

Research Needs

1. Determine characteristics of structures used as natal or maternal dens. Investigate whether den choices vary with the age of the kits and what factors influence a female's choice to change den sites over time.

2. Investigate the reproductive rates of fishers in free-living, non-trapped populations. In addition, study the reproductive rates of females in small populations because these may have suffered loss of genetic variability.

3. Determine the fisher mating system and whether few dominant males do most of the breeding. Determine whether the number of males, and sex ratio, affect the proportion of breeding females.

4. Test the hypotheses that successful hunting during winter leads to high implantation rates and that successful hunting during gestation leads to high embryo survival.

FOOD HABITS AND PREDATOR-PREY RELATIONSHIPS

Principal Prey Species and Diet

Fishers are generalized predators. They eat any animal they can catch and overpower, generally small- to medium-size mammals and birds, and they readily eat carrion and fruits (table 2). The methods used to quantify the diets of carnivores are at best indices of foods eaten. Food items with relatively large proportions of undigestible parts are overrepresented in gastrointestinal (GI) tracts and scats; therefore the remains of small mammals are over

represented compared to large food items (Floyd et al. 1978; Lockie 1959; Scott 1941; Zielinski 1986).

A list of the foods identified from fecal remains or GI tract contents gives little information about where foods were obtained, when they were obtained, or how they were obtained. Almost all of the GI tracts collected for diet studies were obtained from trappers during legal trapping seasons and therefore only provide information on winter diets. Trap bait is commonly found in GI tracts of trapped animals, making it difficult to distinguish between kills initiated by fishers and items obtained as carrion. Trap bait, however, is a legitimate component of fishers' diets during the trapping season because fishers readily eat carrion (Kelly 1977; Powell 1993).

In the following discussion, we use the term "mice" to refer to all small cricetids, including microtines (voles and lemmings). All studies were predominantly winter diets (table 2). It is unfortunate that the only study of the food habits of fishers from Pacific Coast states was limited to the analysis of seven GI tracts from California and appears to have been affected by considerable sampling error due to small sample size. Grenfell and Fasenfest (1979) found a high frequency of "plant" material, a large amount of which was mushroom (false truffles). Black-tailed deer (*Odocoileus hemionus*), cattle, and mice remains also occurred in this sample.

The study of food habits of fishers in the Idaho Rocky Mountains (Jones 1991) has only slightly larger sample sizes: 7 GI tracts and 18 scats. Both GI tracts and scats had high frequencies of occurrence of mammal remains (58% and 68%) and low frequency of occurrence of bird remains (3%, 4%). Ungulate remains, consumed as carrion, were common in both samples (86%, 56%). Remains of insects and other invertebrates were uncommon and vegetation was consumed commonly but probably incidentally to eating prey or in attempts to escape live traps.

For fishers in the Cabinet Mountains of Montana, 50% of the prey remains found in 80 scats were from snowshoe hares (Roy 1991). Mice and other small rodents constituted the next most common prey. Porcupines constituted 5-10% of the prey items eaten and deer carrion constituted less than 5%. Roy (1991) believed that the importance of carrion was underestimated by his scat analyses because the fishers he studied used deer carcasses extensively on several occasions but no scats were collected in those areas.

Snowshoe hares are the most common prey for fishers and have been reported as prey in virtually

Table 2.--Food habits of fishers in five geographic locations. When there are three or more sources of information for a geographic location the range of frequencies of occurrence are provided and when there are only two sources of information commas separate the actual frequencies. The types of samples used are listed under each location.

Food item	California stomach	Idaho GI + scat	Maine New Hampshire New York GI + scat	Manitoba Michigan Minnesota stomach + scat	Ontario GI
Medium-sized prey					
Snowshoe hare	0	29, 50	3-28	19-84	12, 44
Porcupine	0	0, 6	0-26	0-20	20, 35
Small prey					
Mice and voles[15]	37	43, 39	3-50	3-20	9, 16
Shrews and moles[16]	12	0, 0	3-52	0-8	7, 8
Squirrels [17]	12	14, 33	9-25	1-14	0, 4
Birds	0	14, 17	6-30	0-8	11, 23
blue & gray jays	0-7	0	0, 2		
ruffed grouse	0-12	0-7	4, 14		
misc. & unident,[20]	0-19	0-9	2, 7		
Carrion					
White-tailed/black-tailed deer					
+ moose + elk	25	86, 56	2-50	0-28	3, 22
Prey including trap bait					
Muskrat[18]	0	0, 0	0-9	0-1	0, 15
Raccoon[18]	0	0, 0	0-5	0	1, 3
Beaver[18]	0	29, 6	1-17	0	0, 2
Misc. & unident.					
Mammals[19]	100	14, 24	0-30	9-14	2, 45
Vertebrates[21]	88	0, 6	0-4	3-35	12, 13
Arthropods	37	0, 22	0-5	0-2	3, 21
Plant material[22]	100	39, 21	3-37	6-13	18, 61
Sources	1	2	3,4,5,6,7,8,9	10,11,12	13,14

[1] Grenfell and Fosenfest 1979.
[2] Jones 1991.
[3] Coulter 1966.
[4] Arthur et al. 1989o.
[5] Stevens 1968.
[6] Kelly 1977,
[7] Guiliano et al, 1989.
[8] Hamilton and Cook 1955.
[9] Brown and Will 1979,
[10] Roine 1987.
[11] Powell 1977,
[12] Kuehn 1989.
[13] De Vos 1952.
[14] Clem 1977.
[15] Clethrionomys, Microtus, Mus, Napeozopus, Peromyscus, Reithrodontomys, Synaptomys, Zopus.
[16] Blaring, Scolopus, Sorex.
[17] Glaucomys, Sciurus, Tomiasciurus,
[18] Includes bolt.
[19] Miscellaneous mammals (often bait): moles, cottontail rabbit, mink, red fox, American marten, weasels, otter, caribou, fisher, skunk, beaver, muskrat, woodchuck, domestic mammals, unidentified,
[20] Miscellaneous birds: red-breasted nuthatch, thrushes, owls, black-capped chickadee, downy woodpecker, yellow-shafted flicker, sparrows, dark-eyed junco, red-winged blackbird, starling, crow, ducks, grouse eggs, domestic chicken, unidentified.
[21] Miscellaneous vertebrates: snakes, toads, fish, unidentified,
[22] Plant material: apples, winterberries, mountain ash berries, blackberries, raspberries, strawberries, cherries, beechnuts, acorns, swamp holly berries, miscellaneous needles and leaves, mosses, club mosses, ferns, unidentified.

all diet studies (table 2). The species range of the snowshoe hare is coincident with almost the entire fisher species range and, therefore, snowshoe hares are expected to occur frequently in the diets of fishers. The occurrence of snowshoe hare remains in fisher scats ranges from 7% to 84% (table 2), though the California study (Grenfell and Fasenfest 1979) and a study in progress in Connecticut (Rego, pers. comm.) did not discover hare in the diet. Surprisingly, raccoon (*Procyon lotor*) are common prey in Connecticut. Fisher populations across Canada cycle in density approximately 3 years behind the hare cycle (Bulmer 1974, 1975) and as the snowshoe hare population declines, snowshoe hares decrease in fishers' diets (Kuehn 1989).

Understanding the habitat relationships of fisher prey is an important element of understanding fisher ecology. Fishers often hunt in those habitats used by hares (Arthur et al. 1989b; Clem 1977; Coulter 1966; Kelly 1977; Powell 1977, 1978; Powell and Brander 1977) and may direct their travel toward those habitats (Coulter 1966; Kelly 1977; Powell 1977). Hares use a variety of habitat types (Keith and Windberg 1978), but areas with sparse cover appear to be poor hare habitat (Keith 1966). Hares tend to concentrate in conifer and dense lowland vegetation during the winter and to avoid open hardwood forests (Litvaitis et al. 1985). On the Olympic Peninsula of Washington hares appear common in both early and late successional Douglas-fir forests stands, but not mid-successional stands (Powell 1991, unpubl.).

The fisher-porcupine predator-prey relationship has been the subject of considerable study. The importance of porcupines as prey for fishers is reflected in the evolution of the unique hunting and killing behaviors used by fishers to prey on porcupines. Their low build, relatively large body, great agility, and arboreal adaptations make them uniquely adapted for killing porcupines. As a result of these adaptations, fishers have a prey item for which they have little competition. The importance of this should not be underemphasized, even though fishers are found in areas with no porcupines.

Porcupines are important prey for fishers in many places and the frequency of porcupines in diet samples can reach 35% (table 2). Porcupines, however, are seldom as common in fisher diets as snowshoe hares and sometimes they are completely absent. Hares are preferred over porcupines (Powell 1977), presumably because hares are easier and less dangerous to catch. Nonetheless, where porcupines and fishers co-occur, fishers eat porcupines.

Collectively, mice appear in fishers' GI tracts and scats almost as frequently as snowshoe hares. White-footed mice (*Peromyscus leucopus*), deer mice (*P. maniculatus*), red-backed voles (*Clethrionomys gapperi*), and meadow voles (*Microtus pennsylvanicus*) are the most common mice found in fishers' diets and are generally the most common mice in fisher habitat. Mice are probably not as important to fishers as their occurrence in the diet samples indicates. Because they are small, have a relatively large amount of fur and bones, and are eaten whole, mice are over-represented in the GI tracts and scats of fishers. Mice are often active on the surface of the snow during the winter, especially white-footed mice, deer mice, and red-backed voles (Coulter 1966; Powell 1977, 1978), where fishers presumably catch them more frequently than under the snow.

Shrews are found with unexpectedly high frequencies in GI tracts and scats of fishers, since carnivores are usually reluctant to prey on them (Jackson 1961). Shrews are often active during periods of extreme cold (Getz 1961) and, therefore, may sometimes be relatively abundant locally.

Squirrels are common mammals throughout the fisher's range but are eaten less frequently than mice. Red squirrels (*Tamiasciurus hudsonicus*), Douglas squirrels (*T. douglasii*), and flying squirrels (*Glaucomys* spp.) are found over more of the fisher's range and are, therefore, eaten more often than grey and fox squirrels (*Sciurus* spp.). Red squirrels are difficult to catch (Jackson 1961) and fishers probably catch them most often when they sleep in their cone caches. Fishers capture flying squirrels on the ground (Powell 1977) and in nest holes in trees (Coulter 1966). Because most food habits studies are conducted in winter, chipmunks (*Tamias* spp.) and other hibernating ground squirrels (*Spermophilus* spp., *Marmota* spp., and others) are probably underrepresented in the sample.

The remains of deer and other large ungulates have been found in all diet studies of fishers, but in most studies the total volume of deer remains was small in comparison to its incidence (Clem 1977; Coulter 1966; deVos 1952; Powell 1977). Fishers often return to carcasses long after all edible parts are gone and only tufts of hair and skin are left. Some fishers may have deer hair in their digestive tracts and scats almost all winter and still have eaten few meals of venison (Coulter 1966). Kuehn (1989) reported, however, that the amount of fat carried by fishers in Minnesota increased when the number of white-tailed deer (*Odocoileus virginianus*) harvested by hunters in-

creased. Fishers apparently scavenged viscera and other deer parts left by hunters. Kelly (1977), Roy (1991) and Zielinski (unpub. data) documented maternal or natal dens in close proximity to deer carcasses suggesting that females may select dens near carrion.

Some captive fishers eat berries (W. Krohn, pers. comm.) but others generally refuse to eat any kind of fruit or nut (Davison 1975). However, plant material has been found in all diet studies of fishers. Apples are eaten by fishers in New England, where orchards have regrown to forests, but apparently only when other foods are unavailable (W. Krohn, pers. comm.).

Diet Analyses by Age, Season, and Sex

Juvenile fishers eat more fruits than do yearlings or adults (Guiliano et al. 1989). Because juveniles are learning to hunt, they may often go hungry (Raine 1979) and turn to apples and other fruits to ward off starvation. Analyses of diet by season have found little change in diet through the winter (Clem 1977; Coulter 1966) but significant increases in plant material, especially fruits and nuts, in summer (Stevens 1968).

No consistent differences in diet exist between the sexes (Clem 1977; Coulter 1966; Guiliano et al. 1989; Kelly 1977; Kuehn 1989; Stevens 1.968; reviewed by Powell 1993). Anatomical analyses demonstrating that the skulls, jaws, and teeth are less dimorphic than their skeletons (Holmes 1980, 1987; Holmes and Powell 1994a) suggest that dietary specialization of the sexes is unlikely.

Foraging and Killing Behavior

Fishers studied in eastern North America have two distinct components to foraging behavior: search for patches of abundant or vulnerable prey, and search within patches for prey to kill (Powell 1993). Typical of members of the subfamily Mustelinae, fishers hunting within patches of concentrated prey frequently change direction and zigzag. This pattern has been used in dense, lowland-conifer forests where snowshoe hares are found in high densities and in other habitats with high densities of prey (Powell 1977). Between patches of dense prey, fishers travel nearly in straight lines, searching for and heading to new prey patches.

Within habitat patches with high densities of prey, fishers hunt by investigating places where prey are likely to be found (Arthur et al. 1989b; Brander and Books 1973; Coulter 1966; Powell 1976, 1977a, 1978, 1993; Powell and Brander 1977). Fishers will run along hare runs (Powell 1977, 1978; Powell and Brander 1977; Raine 1987) and kill hares where they are found resting or after a short rush attack (Powell 1978). Fishers seeking porcupine dens in upland hardwood forests travel long distances with almost no changes in direction (Clem 1977; Powell 1977, 1978; Powell and Brander 1977). These long upland travels often pass one or more porcupine dens, which fishers locate presumably using olfaction and memory (Powell 1993).

The hunting success rates for fishers are difficult to quantify but appear to be low. There were 14 kills and scavenges along 123 km of fisher tracks in Upper Peninsula Michigan, representing approximately 21 fisher days of hunting (Powell 1993). Seven scavenges were only bits of hide and hair having little food value and 2 kills were of mice (Powell 1993). Thus, the remaining porcupine kill, hare kill, 2 squirrel kills, and scavenging deer were the major results of 21 days of foraging.

Fishers kill small prey such as mice and shrews with the capture bite, by shaking them, or by eating them. They kill squirrels, snowshoe hares, and rabbits with a bite to the back of the neck or head (Coulter 1966; Kelly 1977; Powell 1977, 1978), but a fisher may use its feet to assist with a kill (Powell 1977, 1978). Porcupines are killed with repeated attacks on the face (Coulter 1966; Powell 1977a, 1993; Powell and Brander 1977).

Porcupines deliver quills to fishers but they seldom cause infections or other complications (Coulter 1966; deVos 1952; Hamilton and Cook 1955; Morse 1961; Pringle 1964). All mammals appear to react in the same manner to porcupine quills. Quills carry no poison or irritant and have no characteristics that should cause infection. They are, in fact, covered with a thin layer of fatty acids, which have antibacterial action (Roze 1989; Roze et al. 1990). Porcupines may have evolved antibiotic coated quills to minimize infections from self-quilling when they fall from trees (Roze 1989) or to train individual predators to avoid them and thus to minimize predation (G. Whittler, pers. comm.).

Rabbits, hares, and smaller prey are usually consumed in one meal. Fisher have been observed to cache prey they cannot eat, sometimes in the temporary sleeping dens (Powell 1977). Fishers usually sleep close to large items, such as a deer carcass or a

porcupine, or will pull a porcupine into a hollow log sleeping den (Coulter 1966; deVos 1952; Jones 1991; Kelly 1977; Powell 1977, 1993; Roy 1991).

Management Considerations

1. Snowshoe hares are a major prey item almost everywhere fishers have been studied, including the Rocky Mountains. If this is confirmed from studies elsewhere in the West, managing for hare habitat might benefit fishers if it is not at the expense of denning and resting habitat.

2. In late-successional coniferous forests the presence of high densities of snowshoe hares or porcupines indicates the potential for a fisher population.

Research Needs

1. Determine the seasonal diets of fishers in representative ecoprovinces (Appendix A) in the western United States. In particular, study whether snowshoe hares and porcupines are important fisher prey in the West.

2. Investigate the habitat associations of species found to be common fisher prey and determine how vulnerable they are to fishers in those habitats.

3. Determine whether the management of habitat for primary prey species will increase or decrease habitat suitability for fishers.

4. Investigate whether natal or maternal den choices are influenced by the availability of carrion.

HABITAT RELATIONSHIPS

General Patterns and Spatial Scales

Fishers occur most commonly in landscapes dominated by mature forest cover and they prefer late-seral forests over other habitats (Arthur et al. 1989b; Clem 1977; Coulter 1966; deVos 1952; Johnson 1984; Jones and Garton 1994; Kelly 1977; Powell 1977; Raine 1983; Thomasma et al.1991, 1994). In the Pacific states and in the Rocky Mountains, they appear to prefer late-successional coniferous forests (Buck et al. 1983; Jones 1991; Jones and Garton 1994; Raphael 1984, 1988; Rosenberg and Raphael 1986) and use riparian areas disproportionately more than their occurrence (Aubry and Houston 1992; Buck et al. 1983; Heinemeyer 1993; Higley 1993, unpubl.; Jones 1991; Jones and Garton 1994; Seglund and Golightly 1994, unpubl.; Self and Kerns 1992, unpubl.). However, in

two studies, both in the Rocky Mountains, there were times of the year where young to medium-age stands of conifers were preferred (Jones 1991; Roy 1991). In eastern North America fishers occur in conifer (Cook and Hamilton 1957; Coulter 1966; Hamilton and Cook 1955; Kelly 1977), mixed-conifer, and northern-hardwood forests (Clem 1977; Coulter 1966; Kelly 1977; Powell 1977, 1978). Everywhere, they exhibit a strong preference for habitats with overhead tree cover (Arthur et al. 1989b; Buck et al. 1983; Clem 1977; Coulter 1966; deVos 1952; Johnson 1984; Jones 1991; Jones and Garton 1994; Kelly 1977; Powell 1977, in press; Raine 1983; Raphael 1984, 1988; Rosenberg and Raphael 1986; Thomasma et al. 1991, 1994).

Throughout most of the fisher's range, conifers constitute the dominant late-successional forest types. In the Northeast and Upper Midwest, fishers successfully recolonized and were successfully reintroduced into forests that are predominantly mid-successional, second-growth, mixed-conifer, and hardwood forests. This does not mean that all mid-successional, second-growth forests meet the requirements to support fisher populations. In the Idaho Rocky Mountains, fishers use predominantly old-growth forests of grand and subalpine fir (Jones and Garton 1994). In the Coast Ranges and west-side Cascade forests, fishers are associated with low to mid-elevational forests dominated by late-successional and old-growth Douglas-fir and western hemlock (Aubry and Houston 1992; Buck et al. 1983, 1994; Raphael 1984, 1988; Rosenberg and Raphael 1986). However, in east-side Cascade forests and in the Sierra Nevada fisher occur at higher elevations in association with true fir (*Abies* sp.) and mixed-conifer forests (Aubry and Houston 1992; Schempf and White 1977).

Fishers do not appear to occur as frequently in early successional forests as they do in late-successional forests in the Pacific Northwest (Aubry and Houston 1992; Buck et al. 1983,1994; Raphael 1984, 1988; Rosenberg and Raphael 1986). While some recent work in northern California indicates that fishers are detected in second-growth forests and in areas with sparse overhead canopy (Higley 1993, unpub.; R. Klug, pers. comm.; S. Self, pers. comm.), it is not known whether these habitats are used transiently or are the basis of stable home ranges. It is unlikely that early and mid-successional forests, especially those that have resulted from timber harvest, will provide the same prey resources, rest sites, and den sites as more mature forests.

Studies of fisher habitat have introduced a problem of scale that has not been resolved. Fishers occupy several regional biomes but have been studied most intensively in the forests in the eastern half of North America. Each population studied has been found within one large-scale habitat, such as mixed conifer and northern-hardwood forest or boreal forest. Studies have then investigated selection on the next smaller habitat scale: What stands within the major regional habitat do fishers use? On this scale it has been impossible to parcel portions of population survivorship and fecundity into different stand types. Researchers have therefore assumed that relative time or distance spent in stand types is a measure of habitat preference which, in turn, is a measure of fitness. However, this assumption may not always be true (Buskirk and Powell 1994). For example, fishers may find vulnerable, preferred prey more quickly in some habitats than others and thus may spend more time in habitats in which they find vulnerable prey more slowly (Powell 1994b). No studies have investigated large-scale habitat preferences, as might be found across the pronounced elevational gradients in the western mountains, yet fishers may have critical preferences on this large scale (Aubry and Houston 1992).

There is no universally appropriate scale for analyzing habitat because the scale used must match the questions being asked. Kelly (1977) found that the composition of forests used by a fisher population in New Hampshire was different from the selections made by individual fishers for forest types within their home ranges. Individual fishers appear to use different scales in choosing where to perform different behaviors (Powell 1994b). Where to establish a home range is decided on a landscape scale; where to hunt is decided on a scale of habitat patches; where to rest is decided on a scale of both habitat patches and habitat characteristics within patches. Habitat analyses can be done on several scales but confusing scales can lead to incorrect conclusions (Rahel 1990).

Forest Structure

Habitat requirements of fishers may not always coincide with habitat variables measured, such as predominant tree species and forest types. Buskirk and Powell (1994) hypothesized that physical structure of the forest and prey associated with forest structures are the critical features that explain fisher habitat use, not specific forest types. Structure includes vertical and horizontal complexity created by a diversity of tree sizes and shapes, light gaps, dead and downed wood, and layers of overhead cover. Forest structure should have three functions important for fishers: structure that leads to high diversity of dense prey populations, structure that leads to high vulnerability of prey to fishers, and structure that provides natal and maternal dens and resting sites. Examining fisher habitat use at this level may reconcile the apparently different habitat choices made by eastern and western fishers. Forest structure may also be important to fishers through effects on snow depth, snow compaction, and other snow characteristics (Aubry and Houston 1992; Heinemeyer 1993; Krohn et al., in press).

All habitats used disproportionately by fishers have high canopy closure, and fishers avoid areas with low canopy closure (Arthur et al. 1989b; Coulter 1966; Jones and Garton 1994; Kelly, 1977; Powell 1977, 1978; Raphael 1984; Rosenberg and Raphael 1986; Thomasma et al. 1991, 1994). Fishers also appear to select areas with a low canopy layer that occur in lowland habitat with dense overall canopy cover (Kelly 1977). Late-successional Douglas fir forests of the Pacific Northwest are characterized by multiple layers of cover that create closed-canopy conditions (Franklin and Spies 1991). The studies conducted in this region have concluded that fishers use late-successional forest more frequently than the early to mid-successional forests that result from timber harvest (Aubry and Houston 1992; Buck et al. 1994; Rosenberg and Raphael 1986). Similarly, fishers in the Rocky Mountain study preferred late-successional forests with complex physical structure, especially during the summer (Jones and Garton 1994). However, in areas where late-successional forests are characterized by more open conditions (e.g., ponderosa pine forests maintained by frequent light fires in the Sierra Nevada, McKelvey and Johnson 1992), it is uncertain if fishers will still prefer the closed canopy conditions typical of more mesic ecoregions.

Open, hardwood-dominated forests are frequently avoided throughout the fisher's range (Arthur et al. 1989b; Buck et al. 1983; Clem 1977; Kelly 1977) and, depending on the other available habitats, mixed hardwood-conifer forest types may be avoided (Buck et al. 1983, 1994; Coulter 1966).

Habitat and Prey

In western North America, our ability to characterize fisher foraging habitat on the basis of the habi-

tat of their prey is hampered by the absence of any significant food habitats studies. However, in the Upper Midwest and Northeast, dense lowland forests are preferred by snowshoe hares, and these habitats are selected by fishers. In the Pacific Northwest, the range of the snowshoe hare coincides with the original distribution of Douglas fir forests, where fishers appear to occur most frequently. On the Olympic Peninsula, snowshoe hare sign appears to be associated with late-successional, old-growth Douglas fir/western hemlock stands and with stands of Douglas fir and western hemlock regenerating from logging or from fire and having dense, low branches (Powell 1991, unpubl.). However, others have characterized the habitat of hares on the Olympic peninsula as "semi-open country with brush" (Scheffer 1949). The importance of snowshoe hare in the fisher diet and the habitat relationships of hare, in this region and elsewhere in the West, will need to be determined before the role of hare in fisher habitat choice can be understood.

In eastern North America hunting fishers use both open, hardwood and dense, conifer forest types (Arthur et al. 1989b; Coulter 1966; deVos 1952; Kelly 1977; Powell 1977, 1978; Powell and Brander 1977), but foraging strategies appear to be different in each habitat (Clem 1977; Powell 1977, 1978, 1981b, 1994b; Powell and Brander 1977). Fishers hunting in open, hardwood forests during the winter sometimes alter their directions of travel for small conifer stands where snowshoe hares are abundant (Coulter 1966; Kelly 1977; Powell 1977). Even though fishers may use certain habitats less than expected from their availabilities, those habitats may still have prey important for fishers. In Michigan, fishers used open, hardwood forest significantly less than expected by chance, yet porcupines were found exclusively in those forests. Fishers foraged in a manner that minimized the time and distance traveled in open, hardwood forests while maximizing their chances of finding vulnerable porcupines (Powell 1994b). Kelly (1977) found that fishers in New Hampshire selected habitats with the greatest small mammal (squirrels, shrews, mice) diversity but not the greatest small mammal populations, which are often found in open habitats avoided by fishers. Fishers are opportunistic predators and the availability of vulnerable prey may be more important than high populations of particular prey species.

Because fishers have relatively general diets their potential prey can occur in a variety of forest types and seral stages. However, fishers may forage in different habitats from the ones they use for resting and denning so a complete description of habitat requirements should consider both foraging *and* resting habitat needs. Resting and denning tend to occur in structures associated with late-successional conifer forests (see below), whereas prey can be distributed among a variety of successional stages. Because the types of forests that contain resting and denning sites may be more limiting, these habitats should be given more weight than foraging habitats when planning habitat management.

Snow and Habitat Selection

Fishers appear to be restricted to areas with relatively low snow accumulation. Deep, fluffy snow affects habitat use by fishers (Leonard 1980b; Raine 1983) and may affect distribution, population expansion, and colonization of unoccupied habitat (Arthur et al. 1989b; Aubry and Houston 1992; Heinemeyer 1993; Krohn et al. 1994). When snow is deep and fluffy, causing fishers to leave body drags, fishers move less but travel disproportionately often on snowshoe hare trails and on their own trails (R. Powell, pers. obs.). Fishers will even travel on frozen waterways, which they otherwise avoid, where the snow has been blown and packed by wind (Raine 1983). Where snow is deep, fishers may forage for hares on packed, snowplow drifts along roads that bisect hare habitat (Johnson and Todd 1985).

Snow appears to limit fisher distribution in Washington (Aubry and Houston 1992). On the Olympic Peninsula, and on the west slope of the Cascade Range (primarily the Pacific Northwest Coast and Mountains Ecoprovince, Appendix A), where snowfall is greatest at high elevations, fisher sightings in the past 40 years have been confined to low elevations. On the east slope of the Cascades, where snow is less deep, fisher sightings have been recorded at higher elevations. Krohn et al. (in press), using fisher harvest data, found that indices of fisher recruitment were lower in regions of Maine with deep and frequent snows compared to other areas.

Data from the Rocky Mountains are consistent with avoidance of deep, fluffy snow. Fishers in Idaho and Montana select flat areas and bottoms and avoid midslopes (Heinemeyer 1993; Jones 1991). However, fishers do not show detectable selection or avoidance of ridgetops and steep slopes (Heinemeyer 1993; Jones 1991), although the "selectivity indices" calculated

by Heinemeyer (1993) appear to confuse effects of small sample size with selection. The fishers in all three Rocky Mountain studies (Heinemeyer 1993; Jones 1991; Roy 1991) selected riparian areas, which have relatively gentle slopes, dense canopy, and perhaps protection from snow. Raines' (1983) research indicates that slopes with deep snow should provide poor footing for fishers and should be avoided.

The effect of snow on fisher populations and distribution may also help explain why fisher habitat appears so variable across the species' range. Where snow is deep and frequent, fishers should be expected to be either absent or occur where dense overhead cover intercepts the snowfall (Krohn et al., in press). This hypothesis may explain why fishers in the western United States and the Great Lakes region, where snow tends to be deep, are thought to occur most frequently in late-successional forests (Buck et al. 1994; Harris et al. 1982; Jones 1991; Thomasma et al. 1991) whereas second growth forests are more commonly used by fishers in the northeastern United States in areas where snowfall is relatively low (Arthur et al. 1989b; Coulter 1960). This effect, however, does not explain distribution among habitats during the summer. Additional work is necessary before we can understand how snow, and the interaction between snow and forest structure, influences fisher distribution and habitat choice.

Elevation

In the Pacific States, fishers were originally most common in low to mid-elevational forests up to 2500 m (Aubry and Houston 1992; Grinnell et al. 1937; Schempf and White 1977). In the past 40 years, most sightings of fishers on the Olympic Peninsula and the west slope of the Cascade Range in Washington have been at elevations less than 1000 m but sightings on the east slope of the Cascades where snow is less deep have generally been between 1800 and 2200 m (Aubry and Houston 1992). The highest elevation recorded for an observation of a fisher in California was 3475 m, in the Sierra Nevada (Schempf and White 1977), but most observations in northern California forests have been below 1000 m (Grinnell et al. 1937; Schempf and White 1977; Seglund and Golightly 1994, unpubl.; Self and Kerns 1992, unpubl.). In Montana, fishers released from Wisconsin avoided high elevations (1200-1600 m) and selected low elevations (600-1000 m) after they became established (Heinemeyer 1993).

Use of Openings and Nonforested Habitats

Fishers avoid nonforested areas (Arthur et al. 1989b; Buck et al. 1983, 1994; Coulter 1966; Jones 1991; Jones and Garton 1994; Kelly 1977; Powell 1977, 1978; Roy 1991). Fishers have avoided open areas 25 m across and less in the Midwest (Powell 1977). Large forest openings, open hardwood forests, recent clearcuts, grasslands, and areas above timberline are infrequently used in the West. Existing data are inadequate to assess the use of forest areas with intermediate forest cover resulting from either natural or human-caused disturbances.

Fishers are occasionally found in managed forests with little overhead tree cover, especially in northern California (R. Golightly, pers. comm.; M. Higley, pers. comm.; S. Self, pers. comm.), but the residency, age and reproductive status of these animals is unknown. It is possible that some of these observations may be of foraging animals, given that prey typically associated with nonforested habitats occur in the fisher diet (Jones and Garton 1994). Recently clearcut areas in the Northeast may be used during the summer, when they provide some low overhead cover from brush and saplings, but they are avoided during the winter (Kelly 1977). Rosenberg and Raphael (1986) listed fishers as an "area sensitive" species in northwestern California on the basis of a positive relationship in the frequency of their occurrence and the size of late-successional forest stands. This relationship suggests that, at least for northwestern California, as forested landscapes become more fragmented with openings fishers are less prevalent.

Aversion to open areas has affected local distributions and can limit population expansion and colonization of unoccupied range (Coulter 1966; Earle 1978). An area of farmland in Upper Peninsula Michigan delayed expansion of the population to the north by at least 15 years (R. Powell, pers. obs.) and the Pennobscot River delayed expansion of fishers to eastern Maine for over a decade (Coulter 1966).

Habitat Use by Sex, Age, and Season

There are few seasonal or sexual variations noted in the literature on habitat preferences of fishers. Female fishers in the Northeast may be less selective in their use of habitats during summer than during winter, especially for resting habitat (Arthur et al. 1989b; Kelly 1977). Male fishers in the mountains of

northern California may restrict access of females to preferred habitat that lack hardwoods (Buck et al. 1983). In Idaho, both sexes select late-successional conifer forests during summer but preferred young forests during the winter (Jones and Garton 1994). This was more likely due to a change in prey used during these seasons than to the influence of snow. Some change in habitat preference is caused by avoidance of open habitats that exist in winter but not in summer. Open habitat vegetated with young, deciduous trees and shrubs (typical of recently harvested areas in the East) can be used by fishers in summer (Kelly 1977) but are completely open with no overhead cover in winter.

Resting Sites

Fishers use a variety of resting sites. Most resting sites are used for only one sleeping or resting bout, but a fisher often will rest in the same site for many days, especially when it is close to a large food item, like carrion (R. Powell, pers. obs.), or during severe weather (Coulter 1966; deVos 1952; Powell 1977). Occasionally, individuals may use a site more than once (e.g., Jones 1991; Reynolds and Self 1994, unpubl.) and sometimes more than one individual will use the same resting site (Reynolds and Self 1994, unpubl.). Fishers often approach resting sites very directly, indicating that sites are remembered (deVos 1952; Powell 1993). Live trees with hollows, snags, logs, stumps, "witches' brooms," squirrel and raptor nests, brush piles, rockfalls, holes in the ground, and even abandoned beaver lodges have been reported as rest sites during various seasons (Arthur et al. 1989b; Coulter 1966; deVos 1952; Grinnell et al. 1937; Hamilton and Cook 1955; Powell 1977, 1993; Pringle 1964). The canopies of, or cavities within, live trees are the most commonly used rest sites reported in eastern and western studies (Arthur et al. 1989b; Buck et al. 1983; R. Golightly, pers. comm; Jones 1991; Krohn et al. 1994; Reynolds and Self 1994, unpubl.). In the published western studies, logs were of secondary importance, followed by snags (Buck et al. 1983; Jones 1991). The average diameters of trees used as resting sites were 55.8 cm in Idaho (Jones 1991), and 114.3 cm in northwestern California (Buck et al. 1983). Arthur et al. (1989b) located 180 rest sites of 22 fishers in Maine. Tree "nests" in balsam firs (resting sites on top of branches or in witches' brooms) were commonly used all year. Burrows, especially those of woodchucks (*Marmota monax*), were used most commonly in winter, and cavities in trees were used most commonly in spring and fall. This pattern of rest site use suggests that temperature affects resting site choice and that sites are chosen for warmth and insulation in winter and perhaps to prevent overheating in summer. This conclusion is also supported by the observation that fisher use of logs increases significantly during the winter in Idaho (Jones 1991).

During the winter, fishers sometimes use burrows under the snow with one or more tunnels leading 0.5 to 2.0 m to a larger, hollowed space under the surface of the snow (Coulter 1966; deVos 1952; Powell 1977). Arthur et al. (1989b) reported no use of snow dens by fishers in southcentral Maine, where snow is generally not deep. They did find that fishers tunneled up to 1.5 m through snow to get to ground burrows and they suggested that use of these snow dens may be exaggerated in the literature. Snow dens excavated in Upper Peninsula Michigan were not connected to ground burrows (Powell 1993).

Resting sites reported in studies in the western United States tend to occur predominantly in closed canopy stands. Jones (1991) analyzed canopy closure at 172 rest sites in Idaho and found that fishers preferred to rest in stands that exceeded 61 percent canopy closure during summer and winter, and avoided stands with less than 40 percent closure. Canopy closure at 34 rest sites in northcentral California averaged 82% (Reynolds and Self 1994, unpubl.).

Fishers are more selective of habitat for resting sites than of habitat for foraging. Researchers working in the Rocky Mountains, the Upper Midwest, and the Northeast in the United States have all found that fishers choose lowland-conifer forest types for resting significantly more often than for traveling or foraging (Arthur et al. 1989b; Jones and Garton 1994; Kelly 1977; Powell 1994b). As noted above, fisher prey may be found in a variety of forest types and seral stages. However, resting and denning tends to occur in large trees, snags and logs that are normally associated with late-successional conifer forests. Fishers in the eastern United States find these structures within some second-growth forests (Arthur et al. 1989b), but with the exception of a few observations of fishers using residual snags in early successional forest in California (S. Self, pers. comm.), there are no data in the West to determine how these components are used when they occur in other than late-successional stands. Because the types of forests that normally contain resting and denning sites may be more limiting than foraging habitat within the fisher

range in the West, they should receive special consideration when planning habitat management.

Management Considerations

1. In the western mountains, fishers prefer late-successional forests (especially for resting and denning) and occur most frequently where these forests include the fewest large nonforested openings. Avoidance of open areas may restrict the movements of fishers between patches of habitat and reduce colonization of unoccupied but suitable habitat. Further reduction of late-successional forests, especially fragmentation of contiguous areas through clearcutting, could be detrimental to fisher conservation.

2. Large physical structures (live trees, snags, and logs) are the most frequent fisher rest sites, and these structures occur most commonly in late-successional forests. Until it is understood how these structures are used and can be managed outside their natural ecological context, the maintenance of late-successional forests will be important for the conservation of fishers.

Research Needs

1. Replicate studies of habitat relationships within ecoprovinces (Appendix A) of the mountainous western United States.

2. Investigate the interaction between snow characteristics (depth, density, and frequency), elevation, and forest age/structure on distribution and habitat associations.

3. Determine whether resting and denning is limited to structures in late-successional forest stands.

4. Explore the importance of riparian areas to fisher habitat use in representative ecoprovinces.

5. After food habits studies are conducted, determine the habitat relationships of primary prey within ecoprovinces. Also, determine how forest structure mediates prey availability.

HOME RANGE

Fishers are solitary (Arthur et al. 1989a; Coulter 1966; deVos 1952; Powell 1977; Quick 1953) and appear to avoid close proximity to other individuals (Arthur et al. 1989a; Powell 1977). They probably maintain knowledge of the location of other individuals primarily via scent marking; however, direct contact and overt aggression has been documented

(Arthur et al. 1989a; Coulter 1966; Kelly 1977; Leonard 1986; Powell 1977). The criteria fishers use when establishing a home range are unknown, but the density of vulnerable prey probably play an important role. Tracking data indicate that fishers use most intensively those parts of their home ranges that have high prey densities, and that these areas change (Arthur et al. 1989a; Coulter 1966; Powell 1977).

Home Range Size

Early estimates of fishers' home ranges from tracking data were substantially larger and less accurate than estimates derived more recently from radio-telemetry data (table 3). There is considerable variation in estimates of home range sizes, due in part to different researchers using different methods and treating data differently, in part to most methods of quantifying home ranges being inadequate, and in part to true variation. Recently developed fixed-kernel estimators quantify better than any other available methods both the outlines of home ranges and the distributions of use within home ranges (Seaman 1993; Silverman 1990).

Despite the limits of convex polygon and harmonic mean home range estimators, they have provided most of the information available about fishers' home ranges. There are no apparent geographical patterns in home range sizes, but male home ranges are larger than female home ranges (table 3). In table 3, we have calculated a mean home range area for each sex. Because methods were not consistent between studies, this figure can only be used for general comparisons and therefore includes no measure of variation. The mean home range size for adult male fishers is 40 km^2 (range 19-79), nearly three times that for females (15 km^2; range 4-32). This difference in size between male and female home ranges is greater than that expected from differences between the sexes in energy requirements, or food requirements, calculated from body size. Energy requirements are proportional to W $^{0.75}$, where W is a mammal's weight (McNab 1992). Because male fishers average slightly less than twice as heavy as females (Powell 1993), their energy requirements should be approximately 1.5-1.7 times greater than the energy requirements of females.

Because the territories of male fishers are large, hundreds of square kilometers of suitable habitat may be necessary to maintain sufficient numbers of males to have viable populations. Modeling popula-

tion viability is premature at this point. However, if a viable population has an effective size as small as 50 (Shaffer 1981), half of which is male fishers all of whom breed, then managed areas in the West may need to be at least 600 km² in California (based on Buck et al. 1983) to 2000 km² in the Rocky Mountains (based on Jones 1991) of contiguous, or interconnected, suitable habitat. Not all males and females breed, and minimal viable population size may be larger than 50. Therefore, managed areas likely need to be larger than these estimates. It is unknown whether the habitat is best distributed in an unbroken block, or, a dendritic pattern of wide and connected riparian areas.

There are several potential explanations (not mutually exclusive) for the disproportionate sizes of male and female home ranges. First, males may have energy requirements greater than expected from

Table 3.--Home range sizes (in km²) estimated for fishers. Figures given are means ± standard deviations. The overall mean was calculated by using only one figure for each sex in each study (modified from Powell 1993).

Male	N	Female	N	Location	Method and comments	Source
20 ± 12	3	4.2	1	California	Convex polygons adults with >20 locations females all year males within the breeding season	Buck et al. 1983
23 ± 12	4	6.8	2	California	Convex polygons adults + juveniles females all year males within the breeding season	Buck et al. 1983
16 ± 6	2			California	Convex polygon biased to underestimate	Self and Kerns 1992
79 ± 35	6	32 ± 23	4	Idaho	90% harmonic mean adults + juveniles	Jones 1991
33 ± 25	7	19 ± 12	6	Maine	Convex polygon adults only May-December	Arthur et al. 1989a
27 ± 24	7	16 ± 12	6	Maine	90% harmonic mean adults only May-December	Arthur et al. 1989a
50 ± 40	7	31 ± 23	6	Maine	99% harmonic mean adults only May-December	Arthur et al. 1989a
35	1	15	1	Michigan	Convex polygon adults only winter	Powell 1977
85	2	17	7	Montana	Adaptive kernel non-breeding	Heinemeyer 1993
19 ± 17	3	15 ± 3	2	New Hampshire	Convex polygon adults only all year	Kelly 1977
26 ± 17	3	15 ± 6	3	New Hampshire	Convex polygon subadults only all year	Kelly 1977
23 ± 16	6	15 ± 5	5	New Hampshire	Convex polygon adults + subadults all year	Kelly 1977
49 ± 37	2	8 ± 4	5	Wisconsin	Convex polygon adults with >25 locations all year	Johnson 1984
39 ± 27	4	8 ± 4	7	Wisconsin	Convex polygon adults + juveniles all year	Johnson 1984
40	57	15	55		Mean	

body size and therefore need disproportionately larger home ranges. There is no support, however, for this hypothesis from laboratory research or field estimates of metabolic rates for fishers or other members of the subfamily Mustelinae (Buskirk et al. 1988; Casey and Casey 1979; Moors 1977; Powell 1979a, 1981b; Worthen and Kilgore 1981). Second, the actual areas used by males and females may be proportional to body size, though areas within home range outlines are not. Home ranges of male and female fishers do overlap extensively. In other mustelines, however, males spend minimal time within the home ranges of females encompassed within their own ranges (Erlinge 1977; Gerell 1970). No published data quantify the intensity of home range use by fishers. Third, males and females may space themselves to gain access to different resources: female priority is access to food whereas male priority is access to females. This has been shown to be the case for other mammals, including other mustelines (Erlinge and Sandell 1986; Ims 1987, 1988a, 1988b, 1990; Sandell 1986), and Sandell (1989) has hypothesized this to be the case for solitary carnivores, such as fishers. Fourth, males wander widely during the breeding season (Arthur et al. 1989a) and some of the data used to calculate the mean value for males includes these extra-territorial forays.

Monthly home range of males are greatly enlarged during the breeding season but home ranges of females are not (Arthur et al. 1989a; Johnson 1984). Because male fishers travel so widely during the breeding season, Arthur et al. (1989a) and Buck et al. (1983) excluded estimated locations made during the breeding season when they estimated home range sizes (table 3).

Seaman (1993) hypothesized that male and female mammals have equal lifetime reproductive costs. For male fishers, large body and home range sizes are reproductive costs. If these costs for males were equal to the high reproductive costs for females of raising litters, then home ranges sizes for males and females should be equal. Males, therefore, may forage less intensively throughout their home ranges. Monthly home ranges for fishers are significantly smaller than yearly home ranges and monthly home ranges of females tend to be smaller than those of males (Kelly 1977).

Territoriality

In most populations studied, including populations in California and Montana, fishers appear to exhibit intrasexual territoriality: home ranges overlap little between members of the same sex but overlap is extensive between members of opposite sexes (Arthur et al. 1989a; Buck et al. 1983; Heinemeyer 1993; Johnson 1984; Kelly 1977; Powell 1977, 1979a). Because territories of males are large, a male's territory may overlap territories of more than one female. How territories are maintained is not known. Little overt aggression has been documented between individuals and fishers undoubtedly communicate by scent marking. During the winter, fishers often walk along the tops of logs and large stumps and sometimes walk over and apparently drag their bellies and urinate on small stumps or mounds of snow (Leonard 1986; Powell 1977, 1993). Sometimes, during the breeding season, fishers leave black, tarry marks. These marks resemble feces resulting from rich meals of meat with little fur and bones but do not smell like feces. Fishers also urine mark at the entrances to resting sites and on large carcasses they are scavenging (Pittaway 1978, 1984; Powell, unpubl. data). When logs are moved from one individual's cage to another, the recipient will often rub its abdomen on the log (W. Krohn per. comm.).

Directed agonistic behavior has been observed between a captive adult female fisher and her young, among the young within captive litters five months old and older, and between two captive adult female fishers (Coulter 1966; Kelly 1977; Powell 1977). Arthur et al. (1989a) found male fishers with wounds, and Leonard (1986) examined the carcass of a male fisher with the canine of another fisher in its back.

Some researchers have suggested that intrasexual territoriality in carnivores occurs when large sexual dimorphism permits the two sexes to have different diets. However, this hypothesis has consistently been refuted for fishers, martens, and other mustelines (Clem 1977; Coulter 1966; Erlinge 1975; Holmes 1987; Holmes and Powell 1994; Kelly 1977; King 1989; Tapper 1976, 1979; reviewed by Powell 1994a). Patchily distributed prey is predicted to lead to low costs of sharing a territory with a member of the opposite sex (Powell 1994a). This cost is balanced by reduced chances of reproductive failure for males. Territorial behavior may not be a species-specific characteristic. From very low to very high prey population densities, the following pattern of change in fisher spacing is predicted (Powell 1994a):

transient → individual territories, decreasing in size → intrasexual territories, decreasing in size → extensive home range overlap.

Management Considerations

1. Fishers, especially males, have extremely large home ranges and the largest ranges may occur in the poorest quality habitat. The management of areas large enough to include many contiguous home ranges will probably have the best chance of conserving fisher populations.

Research Needs

1. Use fixed or adaptive kernel methods to determine home range sizes, and describe use areas therein, for males and females in representative ecoprovinces.

2. Evaluate the effects of prey densities and forest composition on home range size, shape, and composition.

3. Determine whether landscape features (i.e., topographic position, elevation within watershed) influence home range locations.

MOVEMENTS

Activity Patterns

Typical of mustelines, fishers have small numbers of activity periods (1 to 3) during a 24-hour period (Powell 1993). They are active day or night, when they are hungry or when their predominant prey is active (Powell 1993), but they often have peaks in activity around sunrise and sunset (Arthur and Krohn 1991) or during the night (deVos 1952). During all seasons, fishers are least active during midday and in winter fishers are often inactive in the middle of the night (Arthur and Krohn 1991; Johnson 1984; Kelly 1977). Fishers are most active during all daylight hours during summer and least active during winter (Johnson 1984; Kelly 1977). No significant difference in activity patterns has been noted between the sexes.

Movement Patterns

Fishers can travel long distances during short periods of time but travel, about 5-6 km per day on the average (Arthur and Krohn 1991; Johnson 1984; Jones 1991; Kelly 1977; Powell 1993; Roy 1991). Adult males are the most mobile, adult females are least mobile and subadults (<21 months old) of each sex are intermediate. All fishers travel longer distances dur-

ing active periods in winter than in summer. Mobility of adult females appears to peak prior to parturition (Kelly 1977; Roy 1991) and then declines through the autumn months. The restricted mobility of females during summer may be caused by having dependent young and may explain why subadult females are more mobile than adult females.

All *Martes* species have clear adaptations for arboreality (Holmes 1980; Leach 1977a, 1977b; Sokolov and Sokolov 1971), partially due to their relatively unspecialized limb anatomy (Holmes 1980; Leach 1977a, 1977b). Fishers climb high into trees to reach holes and possibly to reach prey (Coulter 1966; Grinnell et al. 1937; Leonard 1980a; Powell 1977). Fishers in California were observed to travel from tree to tree to avoid dogs and hunters, sometimes leaping great distances from the branches of one tree to the branches of the next (Grinnell et al. 1937). Nonetheless, fishers are less arboreal than the popular literature claims (Coulter 1966; deVos 1952; Holmes 1980; Powell 1977, 1980; Raine 1987). In the Midwest and Northeast, almost all activity is terrestrial, and in boreal forests fishers may never climb trees while foraging (Raine 1987). Male fishers, who are significantly larger than females, are less adept at climbing (Pittaway 1978; Powell 1977).

Dispersal

Though independent from their mothers starting in the fall, young fishers do not disperse from their mothers' home ranges until mid to late winter (Arthur 1987; Arthur et al. 1993). At age 9 months, few juveniles have established their own home ranges but by age one year, most have (W. Krohn, pers. comm.). In most mammals, males disperse farther than do females and females may remain in or near their mothers' home ranges for their entire lives (Greenwood 1980). The data of Arthur (1987) and Paragi (1990) are not entirely consistent with this pattern because both males and females dispersed similar distances. Juveniles dispersed 10-16 km from their mother's range in Maine (Paragi 1990). In Idaho, two, 1-year-old males established ranges after moving 26 and 42 km, respectively. Because movements occur frequently along forested riparian areas (Buck et al. 1983; Heinemeyer 1993; Jones 1991), it is likely that dispersal occurs in these areas as well. Buck et al. (1983) thought that forested saddles between drainages were important linkages for fisher movements, although habitat selection during dispersal

has not been studied. Large open areas retard population expansion (Coulter 1966; Earle 1978), perhaps because dispersing individuals are inhibited from entering nonforested areas.

Movements and Reintroduction

Movements of reintroduced animals may provide an indication of the maximum distances that fishers from extant populations may move. In West Virginia (Pack and Cromer 1981), fishers moved an average of 43.7 km (90 km maximum) from the release site and movements as far as 98 km were noted in a Wisconsin reintroduction (Olsen 1966). In Montana, males and females moved up to 102 and 56 km (Weckwerth and Wright 1966) and up to 71 and 163 km (Roy 1991) from their release sites.

All fisher reintroductions except one were done during winter. Irvine et al. (1962, 1964) recommended winter reintroductions. Fishers can be trapped easily during winter and it was believed that females would not travel far as parturition approached. Nonetheless, fishers reintroduced during winter travel long distances (Proulx et al. 1994; Roy 1991) and may be subject to predation (Roy 1991).

Proulx et al. (1994) released fishers in the parklands of Alberta during both late winter and summer. Fishers released during winter traveled significantly longer distances and had significantly higher mortality than the fishers released during summer. Most fishers released in summer established home ranges close to their release sites, whereas this was not the case for the fishers released during winter. Proulx et al. recommended that more experiments be conducted to find optimal release times but that, in the mean time, fishers should be released in June when possible.

Management Considerations

1. Fishers are capable of moving long distances, but movements may be restricted in landscapes with large nonforested openings. The maintenance of contact between individuals and subpopulations and the recolonization of unoccupied habitat may be facilitated by reducing the size of openings.

2. Where reintroductions are necessary, conduct them during the summer until additional research dictates otherwise.

3. Fishers probably prey on snowshoe hares in the West. Where fishers are translocated to areas with cyclic snowshoe hare populations, release them during the increase phase of the hare cycle.

Research Needs

1. Investigate the seasonal movement patterns by adults of both sexes in representative ecoprovinces in the West.

2. Study the dispersal behavior of juvenile fishers. Evaluate the dispersal distances, the habitat characteristics (landscape and stand scales), and topographic features used and avoided during dispersal.

3. Test the hypothesis that dispersing juveniles are less selective of habitat than adults.

4. Investigate movements of fishers following translocation to understand how and where fishers establish home ranges.

COMMUNITY INTERACTIONS

Food Webs and Competition

The fisher, as a predator, is predominantly a secondary consumer. Occasionally, however, fishers eat berries and eat other carnivores making them both primary and tertiary consumers as well. In the community of organisms living in the northern forests of North America, fishers most clearly take the role of predators on small- to medium-size mammals and birds. Depending on the specific community, fishers may potentially compete with coyotes, foxes, bobcats, lynx (*Lynx canadensis*), American martens, wolverines (*Gulo gulo*), and weasels. Although this competition has not been documented and there is no direct evidence for its occurrence, the competitive interactions between fishers and American martens, in particular, have been the subject of some discussion.

Fishers and American martens are the only medium-sized, northern predators that are agile in trees and also are elongate and are able to explore hollow logs, brush piles and holes in the ground for prey. The geographic distributions of these species overlap considerably (Douglas and Strickland 1987; Strickland and Douglas 1978), but in the West martens tend to occur at higher elevations than fishers (Buskirk and Ruggiero, Chapter 2; J. Jones, pers. obs.; Schempf and White 1977). However, martens and fishers are sympatric in areas in the southern Sierra Nevada (W. Zielinski, pers. comm.) in northern Idaho (J. Jones pers. comm.), and undoubtedly in other areas as well. Fishers are larger than martens and are able to kill a larger range of prey. Whenever two gen-

eralized predators differ predominantly in size and lack specializations, the larger predator can prey upon the entire range of prey available to the smaller plus it can prey on larger prey. Thus, in periods of severe competition, the larger predator will prevail (Wilson 1975). However, where fishers and marten coexist it may be via niche partitioning (Rosenzweig 1966) because marten are small enough to be able to specialize on hunting voles, especially *Clethrionomys* sp., under snow (Buskirk 1983; Martin 1994). Clem (1977) found dietary overlap between fishers and martens in Ontario to be most profound during the winter but concluded that competition for food did not likely result in competitive exclusion. In the northeastern United States, Krohn et al. (1994) hypothesize that the inverse relationship between captures of fishers and martens by commercial trappers may result from an interaction between competitive displacement of marten by fisher and the avoidance of areas with deep and frequent snowfalls by fishers but not martens.

Fishers may compete with bobcats and especially lynx, because snowshoe hares are the fishers' predominant prey in many places. Presumably the foraging patterns used by fishers differ greatly enough from those used by the felids that competition is minimized. Fisher populations in Canada cycle in response to and about 3 years out of phase from snowshoe hare populations (Bulmer 1974, 1975). Fishers cycle 1-2 years out of phase from lynx (Bulmer 1974, 1975), because low hare populations affect fisher populations through increased juvenile and adult mortality but affect lynx populations primarily through increased juvenile mortality and decreased reproduction. However, these effects will be minimized in the United States where hare populations do not cycle (Dolbeer and Clark 1975; Koehler 1990). Fishers have been reestablished in areas inhabited by foxes, coyotes, bobcats, and lynx, which suggests that competition with these other predators is not limiting to fisher populations.

Where fishers and porcupines occur together, fishers have little competition with other predators for porcupines. Other predators do kill porcupines occasionally (Roze 1989) and mountain lions (*Puma concolor*) may kill porcupines more than occasionally (Maser and Rohweder 1983). Fishers, however, have unique adaptations for killing porcupines and no other predators have been implicated as regulators of porcupine populations (Powell 1977, 1993; Powell and Brander 1977; Roze 1989).

Predation on Fishers

As far as is known, adult fishers are not regularly subject to predation. The occasional fishers reported as killed by other predators were probably ill, old, otherwise in poor health, or lacking in appropriate behavior, making them easy and not dangerous to kill. Four of 20 radio-collared fishers in California died of wounds inflicted by predators or other fishers (Buck et al. 1983). Two fishers were killed by mountain lions in California (Grinnell et al. 1937) and 3 of 21 animals studied by Jones (1991) were killed by predators. Heinemeyer (1993) and Roy (1991) reported high predation rates on fishers translocated from Minnesota and Wisconsin to northwestern Montana. Predators there included bears (*Ursus* spp.), coyotes, golden eagles, lynx, mountain lions, and wolverines. The introduced fishers may have been at risk due to their unfamiliarity with the predators, forests, topography, snow conditions, and prey in the western mountains.

Although Heinemeyer's and Roy's results may give little insight into predation on fishers under natural conditions, their results give significant insight into design of reintroductions. Special steps may be necessary when fishers are released into habitat very different from that in which they were captured, especially when the new habitat supports several predators not known to the fishers in their original habitat. If fishers are released in summer, as suggested by Proulx et al. (1994), they may not travel long distances exposing themselves to other predators. When movements are reduced, fishers establish home ranges promptly and probably learn important local landscape features quickly. Fishers can be released into holding cages where they are housed for an habituation period, but Heinemeyer (1993) found that such "soft" releases in early winter did not affect subsequent movements and activity by released fishers. Alternatively, fishers might be released into areas with low populations of other predators, especially mountain lions and golden eagles.

It is possible that forest fragmentation may affect predation on fishers by other predators. If fragmentation causes fishers to travel long distances through unfamiliar habitat (especially unpreferred habitat) in search of mates, the fishers might be subject to predation.

Management Considerations

1. Animals reintroduced from the same, or nearby, ecoprovinces and into areas with low populations of

potential fisher predators have the best chance of survival.

2. Until the importance of competition between fisher and American marten is determined, it appears that management for both species on the same areas may not be as successful as exclusive areas for each species.

Research Needs

1. Test the hypothesis that the fragmentation of late-successional forest habitat changes competitive interactions between fishers and their potential predators and competitors.

2. Investigate the niche relationships of marten and fisher where they co-occur and test the hypothesis that snow depth and forest structure mediates competitive interactions.

3. Snowshoe hares may constitute a large proportion of the diet of fishers and lynx. Study the food habits of fishers and lynx where they occur together to assess the potential for direct competition.

CONSERVATION STATUS
Human Effects on Fishers

Humans and fishers interact in a number of ways. First, since before European colonization of North America, fishers have been valued for their pelts (Barkalow 1961; Graham and Graham 1990). Fishers have been trapped for fur and, to a lesser extent, farmed for fur. Second, humans affect fisher populations through forestry practices and other activities that alter the fishers' habitat. Fishers lose resting, denning, and foraging habitat through logging of late-successional forests, clearing of forests for agriculture, and clearing of forests for development. Third, fishers have been used to manage porcupine populations. And, fourth, the fisher is unique to North America and is valued by native and nonnative people as an important member of the complex natural communities that comprise the continent's northern forests. Fishers are an important component of the diversity of organisms found in North America, and the mere knowledge of the fisher's existence in natural forest communities is valued by many Americans. Fishers and their pelts are an important element of some American Indian cultures. For example, on the Hoopa Reservation in northwestern California skins are used to fashion quivers and skirts that are

important ceremonial regalia, and the needs of fisher are considered in forest management (M. Higley, pers. comm.).

The fisher's reaction to humans in all of these interactions is usually one of avoidance. Even though mustelids appear to be curious by nature and in some instances fishers may associate with humans (W. Zielinski, pers. obs.), they seldom linger when they become aware of the immediate presence of a human. In this regard, fishers generally are more common where the density of humans is low and human disturbance is reduced. Although perhaps not as associated with "wilderness" as the wolverine (V. Banci, Chapter 5), the fisher is usually characterized as a species that avoids humans (Douglas and Strickland 1987; Powell 1993).

Trapping

Trapping, with logging, has had a major impact on fisher populations. Fishers are easily trapped and the value of fisher pelts in the past created trapping pressure great enough to exterminate fishers completely from huge geographic areas. Wherever fishers are trapped, populations must be monitored closely to prevent population decrease. In addition to the clear evidence from past population declines, there is evidence from more recent changes in populations in eastern states and provinces (Douglas and Strickland 1987; Kelly 1977; Krohn et al. 1994; Parson 1980; Strickland and Douglas 1978; Wood 1977; Young 1975) and theoretical evidence (Powell 1979b) that small changes in mortality due to trapping can greatly affect fisher populations.

Because fishers are easily trapped, where fisher populations are low they can be jeopardized by the trapping of coyote, fox, bobcat, and marten (Coulter 1966; Douglas and Strickland 1987; Jones 1991; Powell 1993). Wisconsin designated fisher wildlife management areas in the Nicolet and Chequamegon National Forest (approximately 550 km^2 and 1,000 km^2) where land sets for all furbearers were prohibited (Petersen et. al. 1977). During the two years that British Columbia closed the fisher season the incidental capture of fishers exceeded the legal capture the preceding year (V. Banci pers. comm.). The closure of all commercial marten trapping where their range overlaps that of the fisher in Washington and Oregon has been recommended by the Forest Ecosystem Management Assessment Team in a recent EIS (USDA 1994) until the rate of incidental take is considered

to be insignificant. Idaho and Montana each provide modest financial incentive for information about incidentally captured fishers (B. Giddings, pers. comm.; G. Will, pers. comm.). Where commercial trapping of terrestrial carnivores occurs, the threat exists that fishers will be trapped and that their populations could be negatively affected (Powell 1979b).

Forest Management

The extensive, clearcut logging done during the 1800's and early 1900's, together with trapping, decimated fisher populations all over the continent. Because fishers are associated most frequently with relatively unfragmented, late-successional forests, recent clearcut logging continues to affect fisher populations today through its profound effects on forest landscapes. Large nonforested areas are avoided by fishers, especially during the winter, and the fact that extensive areas of the Pacific Northwest have been recently clearcut (e.g., Morrison 1988) may be the reason fisher populations have not recovered in some parts of this region (Aubry and Houston 1992).

The problem for fishers is not with forest openings per se. Fishers evolved in forests where windthrow and fire were common. Small patch cuts, group selection harvests, and small clearcuts can superficially resemble both these disturbances in form and in the pattern of succession that follows. Fishers have been reported to use recently clearcut areas during the summer, when the cover formed by ground vegetation and young trees is dense, and, in the East, they also use young, second-growth forests. Presumably, fishers experience habitat loss when timber harvest removes overstory canopy from areas larger and more extensive than natural windthrow and fire would. Provided there are large patches of late-successional conifer habitat nearby, fisher populations should be able tolerate incidents of stand-replacing disturbances. Small patch cuts interspersed with large, connected, uncut areas should not seriously affect fisher populations. In fact, these small-scale disturbances may increase the abundance and availability of some fisher prey. Large clearcuts and numerous, adjacent, small clearcuts of similar age should seriously limit resting and foraging habitat for fishers during the winter. This, in turn, may limit fisher population size. The effect of uneven-aged timber management practices on fisher habitat have not been studied but are likely to have less effect on fisher habitat than even-aged management. Forestry practices aimed at maximizing wood production and minimizing rotation times will probably have detrimental effects on fisher populations.

For many species, including the fisher, much still needs to be known about how natural populations function. Differences in forest habitats between the Pacific States, the Rocky Mountains, and the forest of the Upper Midwest and Northeast are profound enough to prevent simplistic extrapolations about fisher-habitat relationships. We must learn how fishers use the forests of the western mountains before we can fully understand the components of these forests that are important to fishers.

Conservation Status
in the Western United States

The primary reason for concern about the fishers in the western mountains of the United States is the utter lack of data on the ecology of the species. Only two intensive, radio-telemetry based habitat studies have been published on fishers, one in northwestern California (Buck et. al. 1983) and the other in Idaho (Jones 1991) (table 4). Two additional studies have been completed at about the same locations in Montana (Heinemeyer 1993; Roy 1991) but both individuals studied fishers that were introduced from Wisconsin and Minnesota. Inferences from these studies to extant populations elsewhere in the West may be limited. Only two natal dens and one maternal den have been discovered and described in the West (two of the three were in northwestern California). Only about 100 scats and gastrointestinal tracts have been examined to describe food habits, the majority of which may be unrepresentative of native fisher diets because they came from transplanted individuals in Montana (table 4). Thus, the quantity of data on the ecology of fishers in the West is extremely low. A sizeable amount of unpublished data exist (noted throughout the text above and in Appendix C) but the quality of this information is hard to verify and thus its usefulness is limited. Neither of the studies of native populations have been replicated within their ecoprovinces and entire ecoprovinces (see Appendix A) are without a single representative study (e.g., Georgia-Puget Basin, Pacific Northwest Coast and Mountains, Sierra Nevada, Columbia Plateau, Northern Rocky Mountain Forest). New research is underway in northern California (Reynolds and Self 1994, unpubl.; Seglund and Golightly 1994, unpubl.; Schmidt et al. 1993, unpubl.) and the southern Sierra

Table 4.--The knowledge base for the fisher in the western United States, excluding Alaska, by subject. This includes studies for which the subject was a specific objective of the study; incidental observations are not included. Sample size is number of animals studied, or for food habits, number of scats or gastrointestinal tract contents, unless stated otherwise. Sample sizes for dispersal include only juveniles. Theses and dissertations are not considered separately from reports and publications that report the same data. A total of four studies (*) are represented in this table.

Topic, author	Location	Method	Duration (years)	Sample size
Home range & habitat use				
*Buck et al, 1994	California	Telemetry-convex polygon	1.5	6
*Heinemeyer 1993[1]	Montana/Idaho[2]	Telemetry-adaptive kernel	2	9/10[6]
*Jones 1991	Idaho	Telemetry-harmonic mean	4	10
*Roy 1991[1]	Montana[3]	Telemetry-habit use primarily	2	18
Demography				
Roy 1991[1]	Montana	Mortality and reproduction of transplanted animals	4	32
Food habits				
Grenfell & Fasenfest 1979[4]	California	GI tracts	-	8
Jones 1991	Idaho	GI tracts + scats	4	25
Roy 1991[1]	Montana	Scats	2	80
Dispersal[5]				
Natal dens				
Roy 1991[1]	Montana	Telemetry	2	1
Buck et al. 1983[6]	California	Incidental to study	-	1

[1] Data collected from transplanted individuals.
[2] Adaptive kernel home range calculated from Jones' (1991) data included.
[3] Same locations as Heinemeyer (1993).
[4] From fishers that died during the course of the study by Buck et al. (1983).
[5] No data for western fishers.
[6] Buck et al. (1983) same as Buck et al (1994).

Nevada (W. Zielinski, pers. comm.), but a tremendous amount of additional research is necessary before a responsible conservation strategy can be assembled.

A second reason for concern comes from interpreting the results of the two published studies on native populations in the West. In each case, fishers prefer late-successional coniferous forests: throughout the year in California (Buck et al. 1983) and especially in summer in Idaho (Jones 1991). Late-successional forests provide important benefits for fishers, especially resting and denning habitat. The reduction in this habitat and its increasing fragmentation is part of the reason fishers in the Pacific States are considered by many to be threatened with extirpation and why some have petitioned the U.S. Fish and Wildlife Service to list the fisher under the Endangered Species Act (Central Sierra Audubon Society et al. 1991).

Reintroductions appear not to have augmented populations in western Oregon and recent records of fishers in Washington are uncommon. Since the late 1950's, only one sighting of a fisher has been substantiated on the Olympic Peninsula in Washington,

and that was a fisher killed in a trap in 1969. A fisher killed in the 1990-91 trapping season and a fisher trapped and photographed in 1993 in the Cascade Range are the only other substantiated reports (Aubry and Houston 1992; Aubry, unpub. records). Fishers are probably extirpated on the Olympic Peninsula and are either extirpated or very patchily distributed in meager populations in the rest of western Washington and Oregon.

It is our opinion that the precarious status of the fisher population in Washington and Oregon is related to the extensive cutting of late-successional forests and the fragmented nature of these forests that still remain. Fishers appear sensitive to loss of contiguous, late-successional Douglas fir forests in the Pacific Coast Ranges, west slope of the Cascade Range, and west slope of the Sierra Nevada (Aubry and Houston 1992; Gibilisco 1994; Raphael 1984, 1988; Rosenberg and Raphael 1986), but their habitat associations in more xeric forest types in the Pacific States (e.g., east slope of the Cascades, ponderosa pine forests in the Sierra Nevada) are unknown. We suspect that in Douglas fir forests, late-seral conditions provide the physical structure that allows fishers to hunt

successfully and to find suitable resting and denning sites. Young, second-growth forests may be unable to provide these requirements.

Establishing the reasons for the precarious status of the fisher populations in the Pacific Northwest may not be as important in the short term as making people aware of the status and providing federal protection for the populations. That the populations appear dangerously low should be sufficient to generate protection; discussions and research into the reasons should occur after protection. In our opinion, protection by the states of Washington, Oregon, and California has not been sufficient to improve population status.

The status of fishers in the northern and central Sierra Nevada is unknown but the absence of recent observations suggests they are declining or barely holding steady (Gibilisco 1994). Fisher populations in the northern Rocky Mountains of the United States do not appear to be in as critical condition as those in the Pacific Northwest. Although fishers have not recolonized all of their former range in this region, some healthy fisher populations exist. Fishers were never found much farther south than the Yellowstone region. If trapping seasons are regulated carefully in Montana to prevent overtrapping, fisher populations may slowly expand in Montana and Idaho. If fisher populations are limited by deep snow, however, fishers may never reach high densities in these mountain states.

LITERATURE CITED

Allen, A.W. 1983. Habitat suitability index models: Fisher. U.S. Fish and Wildlife Service; FWS/OBS-82/ 10.45.

Anderson, E. 1970. Quaternary evolution of the genus *Martes* (Carnivora, Mustelidae). Acta Zoologica Fennica. 130:1-133.

Anderson, E. 1994. Evolution, prehistoric distribution and systematics of *Martes.* In: Buskirk, S.W.; Harestad A.; Raphael M., comps, eds. Martens, sables and fishers: biology and conservation. Ithaca, NY. Cornell University Press: 13-25.

Arthur, S.M. 1987. Ecology of fishers in south-central Maine. Orono, ME: University of Maine. Ph.D. thesis. 112 p.

Arthur, S.M.; Cross, R.A.; Paragi, T.F. [et al.]. 1992. Precision and utility of cementum annuli for determining ages of fishers. The Wildlife Society Bulletin. 20: 402-405.

Arthur S.M.; Paragi, T.F.; Krohn, W.B. 1993. Dispersal of juvenile fishers in Maine. Journal of Wildlife Management. 57:868-874.

Arthur, S.M.; Krohn W.B. 1991. Activity patterns, movements, and reproductive ecology of fishers in southcentral Maine. Journal of Mammalogy. 72: 379-385.

Arthur, S.M.; Krohn, W.B.; Gilbert, J.R. 1989a. Home range characteristics of adult fishers. Journal of Wildlife Management. 53: 674-679.

Arthur, S.M.; Krohn, W.B.; Gilbert, J.R. 1989b. Habitat use and diet of fishers. Journal of Wildlife Management. 53: 680-688.

Aubry, K.B.; Houston, D.B. 1992. Distribution and status of the fisher in Washington. Northwestern Naturalist. 73: 69-79.

Balser, D.S. 1960. The comeback of the furbearers. Minnesota Division of Game and Fish. Conservation.Volunteer. 23(134): 57-59.

Balser, D.S.; Longley W.H. 1966. Increase of fishers in Minnesota. Journal of Mammalogy. 47:342-347.

Banci, V. 1989. A fisher management strategy for British Columbia. Victoria, British Columbia: British Columbia Ministry of the Environment, Lands and Parks, Wildlife Branch. Wildlife Bulletin No. B-63.

Barkalow, F.S. 1961. The porcupine and fisher in Alabama archeological sites. Journal of Mammalogy. 42:544-545.

Berg, W.E. 1982. Reintroduction of fisher, pine marten and river otter. In: Sanderson, G.C., ed. Midwest furbearer management. 159-175.

Berg, W.E.; Kuehn D.W. 1994. Return of two natives: Fisher and marten demographics and range in a changing Minnesota landscape. In: Buskirk, S.W.; Harestad, A.; Raphael, M., comps., eds. Martens, sables and fishers: biology and conservation. Ithaca, NY. Cornell University Press: 262-271.

Bensen, D.A. 1959. The Fisher in Nova Scotia. Journal of Mammalogy. 40:451.

Bradle, B.J. 1957. The fisher returns to Wisconsin. Wisconsin Conservation Bulletin. 22(11): 9-11.

Brown, M.K.; Will, G. 1979. Food habits of the fisher in northern New York. New York Fish and Game journal. 26: 87-92.

Brander, R.B.; Books, D.J. 1973. Return of the fisher. Natural History. 82(1): 52-57.

Buck, S.; Mullis, C.; Mossman, A. 1983. Final report: Corral Bottom-Hayfork Bally fisher study. [Unpublished report]: U.S. Department of Agriculture. In cooperation with: Arcata, CA: Humboldt State University.

Buck, S.; Mullis, C.; Mossman, A. 1994. Habitat use by fishers in adjoining heavily and lightly harvested forest. In: Buskirk, S.W.; Harestad, A.; Raphael, M., comps. eds. Martens, sables and fishers: biology and conservation. Ithaca, NY: Cornell University Press: 368-376.

Bulmer, M.G. 1974. A statistical analysis of the 10-year cycle in Canada. Journal of Animal Ecology. 43:701-718.

Bulmer, M.G. 1975. Phase relations in the ten-year cycle. Journal of Animal Ecology. 44: 609-622.

Buskirk, S.W. 1983. The ecology of marten in southcentral Alaska. Fairbanks, AK: University of Alaska. Ph.D. thesis. 131 p.

Buskirk, S.W.; Maderson, P.F.A.; O'Connor, R.M. 1986. Plantar glands in North American Mustelidae. In: Duvall, D.; Miiller-Schwarze, D.; Silverstein, M., eds. Chemical signals in vertebrates, 4, ecology, evolution and comparative biology. New York: Plenum Press: 617-622.

Buskirk, S.W.; Harlow, H.J.; Forrest, S.C. 1988. Temperature regulation in the American marten (*Martes americana*). National Geographic Research. 4: 208-218.

Buskirk, S.W.; Lindstedt, S.L. 1989. Sex biases in trapped samples of Mustelidae. Journal of Mammalogy. 70:88-97.

Buskirk, S.W.; Powell, R.A. 1994. Habitat ecology of fishers and American martens. In: Buskirk, S.W.; Harestad, A.; Raphael, M., comps. eds. Biology and conservation of martens, sables and fishers. Ithaca, NY: Cornell University Press: 283-296.

Casey, T.M.; Casey K.K. 1979. Thermoregulation of arctic weasels. Physiological Zoology. 52:153-164.

Central Sierra Audubon Society [et al.]. 1990. Petition for a rule to list the fisher as endangered. North San Juan, CA: Central Sierra Audubon Society. 26 p.

Clem, M.K. 1977. Food habits, weight changes and habitat selection of fisher during winter. Guelph, Ontario: University of Guelph. M.S. thesis.

Cook, D.E.; Hamilton, W.J., Jr. 1957. The forest, the fisher, and the porcupine. Journal of Forestry. 55: 719-722.

Coulter, M.W. 1960. The status and distribution of fisher in Maine. Journal of Mammology. 41: 1-9.

Coulter, M.W. 1966. Ecology and management of fishers in Maine. Syracuse, NY: Syracuse University, University College of Forestry. Ph.D. thesis.

Crowley, S.K.; Krohn, W.B.; Paragi, T.F. 1990. A comparison of fisher reproductive estimates. In: Transactions of Northeast Section Wildlife Society. 47:36-42.

Crump, D.R. 1980a. Theitanes and dithiolanes from the anal gland of the stoat (*Mustela erminea*). Journal of Chemical Ecology. 6:341-347.

Crump, D.R. 1980b. Anal gland secretion of the ferret (*Mustela putorius forma furo*). Journal of Chemical Ecology. 6: 837-844.

Curtis, J.D. 1941. The silvicultural significance of the porcupine. Journal of Forestry 39: 583-594.

Curtis, J.D. 1944. Appraisal of porcupine damage. Journal of Wildlife Management. 8: 88-91.

Davison, R.P. 1975. The efficiency of food utilization and energy requirements of captive fishers. Concord, NH: University of New Hampshire. M.S. thesis.

deMonte, M.; Roeder, J.J. 1990. Histological structure of the abdominal gland and other body regions in olfactory communication in pine martens (*Martes martes*). Z. Säugetierkunds. 55: 425-427.

deVos, A. 1951. Recent findings in fisher and marten ecology and management. In: Transactions of 16th North American Wildlife Conference. 16: 498-507.

deVos, A. 1952. Ecology and management of fisher and marten in Ontario. Ontario Department of Lands and Forests; Tech. Bull. Wildlife Service 1. 90 p.

Dodds, D.G.; Martell, A.M. 1971. The recent status of the fisher, *Martes pennanti* (Erxleben), in Nova Scotia. Canadian Field-Naturalist. 85: 62-65.

Dodge, W.E. 1977. Status of the fisher (*Martes pennanti*) in the conterminous United States. U.S. Department of the Interior. [Unpubl. rep].

Dolbeer, R.A.; Clark, W.R. 1975. Population ecology of snowshoe hares in the central Rocky Mountains. Journal of Wildlife Management. 39: 535-549.

Douglas, C.W.; Strickland, M.A. 1987. Fisher. In: Novak, M.; Baker, J.A.; Obbard, M.E., comps.,eds. Wild furbearer management and conservation in North America. Toronto, Ontario: Ontario Ministry of Natural Resources: 511-529.

Douglas, W.O. 1943. Fisher farming has arrived. American Fur Breeder. 16: 18, 20.

Eadie, W.R.; Hamilton, W.J., Jr. 1958. Reproduction of the fisher in New York. New York Fish and Game journal. 5: 77-83.

Earle, R.D. 1978. The fisher-porcupine relationship in Upper Michigan. Houghton, MI: Michigan Technical University. M.S. thesis.

Erlinge, S. 1975. Feeding habits of the weasel *Mustela nivalis* in relation to prey abundance. Oikos. 26: 378-384.

Erlinge, S. 1977. Spacing strategy in stoat *Mustela erminea.* Oikos. 28: 32--42.

Erlinge, S.; Sandell, M. 1986. Seasonal changes in the social organization of male stoats, *Mustela erminea:* An effect of shifts between two decisive resources. Oikos. 47:57-62.

Floyd, T.J.; Mech, L.D.; Jordan, P.A. 1978. Relating wolf scat content to prey consumed. Journal of Wildlife Management. 42:528-532.

Franklin, J.F.; Spies, T.A. 1991. Composition, function, and structure of old-growth Douglas-fir forests. In: Ruggiero, L.F; Aubry K.B.; Carey, A.B. comps., eds. Wildlife and vegetation of unmanaged Douglas-fir forests. Gen. Tech. Rep. PNW -285. Portland, OR: U.S. Department of Agriculture, Pacific Northwest Research Station: 71-89.

Gerell, R. 1970. Home range and movements of the mink *Mustela vison* Schreber in southern Sweden. Oikos. 21: 160-173.

Getz, L.L. 1961. Home ranges, territoriality, and movements of the meadow vole. Journal of Mammalogy. 42: 24-36.

Gibilisco, C.J. 1994. Distributional dynamics of American martens and fishers in North America. In: Buskirk, S.W.; Harestad, A.; Raphael, M., comps. eds. Martens, sables and fishers: biology and conservation. Ithaca, NY Cornell University Press: 59-71.

Guiliano, W.M.; Litvaitis, J.A.; Stevens, C.L. 1989. Prey selection in relation to sexual dimorphism of fishers (*Martes pennanti*) in New Hampshire. Journal of Mammalogy. 70: 639-641.

Goldman, F.A. 1935. New American mustelids of the genera *Martes, Gulo,* and *Lutra.* In: Proceedings Biological Society of Washington. 48:175-186.

Graham, M.A.; Graham, R.W. 1990. Holocene records of *Martes pennanti* and *Martes americana* in Whiteside County, northwestern Illinois. American Midland Naturalist. 124: 81-92.

Graham, R.W.; Graham, M.A. 1994. The late quaternary distribution of *Martes* in North America. In: Buskirk, S.W.; Harestad, A.; Raphael, M., comps. eds. Martens, sables and fishers: biology and conservation. Ithaca, NY Cornell University Press: 26-58.

Greenwood, P.J. 1980. Mating systems, philpatry and dispersal in birds and mammals. Animal Behavior. 28:1140-1162.

Grenfell, W.E.; Fasenfest, M. 1979. Winter food habits of fishers, *Martes pennanti,* in northwestern California. California Fish and Game. 65:186-189.

Grinnell, J.; Dixon, J.S.; Linsdale, L.M. 1937. Fur-bearing mammals of California: Their natural history, systematic status and relations to man. Volume 1. Berkeley, CA: University of California. 777 p.

Hagmeier, E.M. 1956. Distribution of marten and fisher in North America. Canadian Field-Naturalist. 70: 149-168.

Hagmeier, E.M. 1959. A re-evaluation of the subspecies of fisher. Canadian Field-Naturalist. 73: 185-197.

Hall, E.R. 1926. The abdominal skin gland of Martes. Journal of Mammalogy. 7:227-229.

Hall, E.R. 1942. Gestation period of the fisher with recommendation for the animals' protection in California. California Fish and Game. 28:143-147.

Hall, E.R. 1981. The Mammals of North America. New York: John Wiley and Sons.

Hamilton, W.J., Jr.; Cook, A.H. 1955. The biology and management of the fisher in New York. New York Fish and Game journal. 2:13-35.

Harris, L.D.; Maser, C.; McKee, A. 1982. Patterns of old growth harvest and implications for Cascades wildlife. In: Transactions of the North American Wildlife and Natural Resources Conference. 47: 374-392.

Heinemeyer, K.S. 1993. Temporal dynamics in the movements, habitat use, activity, and spacing of reintroduced fishers in northwestern Montana. Missoula, MT: University of Montana. M.S. thesis. 158 p.

Higley, J.M. 1993. Hoopa Valley Indian Reservation draft fisher survey report 1992-1993. Hoopa, CA: Hoopa Tribal Forestry; [Unpubl. rep.]. 20 p.

Hine, R.L. 1975. Endangered Animals in Wisconsin. Madison, WE Wisconsin Department of Natural Resources. [Unpubl. rep.].

Hodgson, R.G. 1937. Fisher Farming. Fur Trade Journal of Canada.

Holmes, T. 1980. Locomotor adaptations in the limb skeletons of North American mustelids. Arcata, CA: Humboldt State University. M.A. thesis.

Holmes, T.1987. Sexual dimprohism in North American weasels with a phylogeny of the Mustelidae. Lawrence, KS: University of Kansas. Ph.D. thesis.

Holmes, R.; Powell, R.A. 1994. Morphology, ecology and the evolution of sexual dimorphism in North American *Martes*. In: Buskirk, S.W.; Harestad, A.; Raphael, M., comps. eds. Martens, sables and fishers: biology and conservation. Ithaca, NY: Cornell University Press: 72-84.

Ims, R.A. 1987. Male spacing systems in microtine rodents. American Naturalist. 130: 475-484.

Ims, R.A. 1988a. Spatial clumping of sexual receptive females induces space sharing among male voles. Nature. 335: 541-543.

Ims, R.A. 1988b. The potential for sexual selection in males: effect of sex ratio and spatiotemporal distribution of receptive females. Evolutionary Ecology. 2: 338-352.

Ims, R.A. 1990. Mate detection success of male *Clethrionomys rufocanus* in relation to the spatial distribution of sexually receptive females. Evolutionary Ecology. 4: 57-61.

Ingram R. 1973. Wolverine, fisher and marten in central Oregon. Salem, OR: Oregon State Game Commission; Central Regional Administrative Report No. 73-2.

Irvine, G.W.; Bradle, B.J.; Magnus, L.T. 1962. The restocking of fisher in lake states forests. In: Midwest Fish & Wildlife Conference. 24.

Irvine, G.W.; Magnus, L.T.; Bradle, B.J. 1964. The restocking of fishers in lake states forests. In: Transaction of the North American Wildlife Natural Resource Conference. 29: 307-315.

Jackson, H.H.T. 1961. Mammals of Wisconsin. Madison, WI: University of Wisconsin. 504 p.

Johnson, S.A. 1984. Home range, movements, and habitat use of fishers in Wisconsin. Stevens Point, WI: University of Wisconsin. M.S. thesis.

Johnson, W.A.; Todd, A.W. 1985. Fisher, *Martes pennanti,* behaviour in proximity to human activity. Canadian Field-Naturalist. 99: 367-369.

Jones, J.L. 1991. Habitat use of fisher in northcentral Idaho. Moscow, ID: University of Idaho. M.S. thesis. 147 p.

Jones, J.L.; Garton, E.O. 1994. Selection of successional stages by fishers in northcentral Idaho. In: Buskirk, S.W.; Harestad, A.; Raphael, M., comps. eds. Martens, sables and fishers: biology and conservation. Ithaca, NY. Cornell University Press: 377-387.

Kebbe, C.E. 1961. Return of the fisher. Oregon State Game Commission. Bulletin 16:3-7.

Keith, L.B. 1966. Habitat vacancy during a snowshoe hare decline. Journal of Wildlife Management. 30: 828-832.

Keith, L.B.; Windberg, L.A. 1978. A demographic analysis of the snowshoe hare cycle. Wildlife Monograph. 58:1-70.

Kelly, G.M. 1977. Fisher (*Martes pennanti*) biology in the White Mountain National Forest and adjacent areas. Amherst, MA: University of Massachusetts. Ph.D. thesis. 178 p.

Kelsey, P. 1977. The return of the fisher. New York State Environment. 6(8): 10.

King, C.M. 1975. The sex ratio of trapped weasels (*Mustela nivalis*). Mammal Review. 5:1-8.

King, C.M. 1989. The natural history of weasels and stoats. Ithaca, NY. Cornell University Press. 253 p. Koehler, G.M. 1990. Population and habitat characteristics of lynx and snowshoe hares in north central Washington. Canadian Journal of Zoology. 68: 845-851.

Krefting, L.W.; Stoeckeler, J.W.; Bradle, B.J. [et al.]. 1962. Porcupine-timber relationships in the lake states. Journal of Forestry. 60: 325-330.

Krohn, W.B.; Arthur, S.M.; Paragi, T.F. 1994. Mortality and vulnerability of a heavily trapped fisher population. In: Buskirk, S.W.; Harestad, A.; Raphael, M., comps. eds. Martens, sables and fishers: biology and conservation. Ithaca, NY: Cornell University Press: 137-145.

Krohn, W.B.; Elowe, K.D.; Boone, R.B. [In press]. Relations among fishers, snow, and martens: development and evaluation of two hypotheses. Foresty Chronicle.

Kuehn, D.W. 1989. Winter foods of fishers during a snowshoe hare decline. Journal of Wildlife Management. 53: 688-692.

LaBarge, T.; Baker, A.; Moore, D. 1990. Fisher (*Martes pennanti*): Birth, growth and development in captivity. Mustelid and Viverrid Conservation. 2:1-3.

Laberee, E.E. 1941. Breeding and reproduction in fur bearing animals. Fur Trade Journal of Canada.

Leach, D. 1977a. The forelimb musculature of marten (*Martes americana* Turton) and fisher (*Martes pennanti* Erxleben). Canadian Journal of Zoology. 55:31-41.

Leach, D. 1977b. The description and comparative postcranial osteology of marten (*Martes americana* Turton) and fisher (*Martes pennanti* Erxleben): the appendicular skeleton. Canadian Journal of Zoology 55:199-214.

Leonard, R.D. 1980a. In: Douglas, C.W; Strickland, M.A., eds. Transactions of 1979 Fisher Conference. Ontario Ministry of Natural Resources. [Unpubl. rep.]. 15-25.

Leonard, R.D. 1980b. Winter activity and movements, winter diet and breeding biology of the fisher in southeast Manitoba. Winnipeg, Manitoba: University of Manitoba. M.S. thesis.

Leonard, R.D. 1986. Aspects of reproduction of the fisher, *Martes pennanti,* in Manitoba. Canadian Field-Naturalist. 100: 32-44.

Litvaitis, J.A.; Sherburne, J.A.; Bissonette, J.A. 1985. Influence of understory characteristics on snowshoe hare habitat use and density. Journal of Wildlife Management. 49: 866-873.

Lockie, J.D. 1959. The estimation of the food of foxes. Journal of Wildlife Management. 23: 224-227.

Lomnicki, A. 1978. Individual differences between animals and natural regulation of their numbers. Journal of Animal Ecology. 47: 461-475.

Lomnicki, A. 1988. Population biology of individuals. Princeton, NJ: Princeton University Press. 223 p.

Maser, D.; Rohweder, R.S. 1983. Winter food habits of cougars from northeastern Oregon. Great Basin Naturalist. 43: 425-428.

May, R.M. 1973. Stability and complexity in model ecosystems. Princeton, NJ: Princeton University Press.

Martin, S.K. 1994. Feeding ecology of American martens and fishers. In: Buskirk, S.W.; Harestad, A.; Raphael, M., comps. eds. Martens, sables and fishers: biology and conservation. Ithaca, NY: Cornell University Press: 297-315.

McKelvey, K.S.; Johnston, J.D. 1992. Historical perspectives on forests of the Sierra Nevada and the transverse ranges of southern California: forest conditions at the turn of the century. In: Verner, J.; McKelvey, K.S.; Noon, B.R., comps., eds. The California Spotted Owl: a technical assessment of its current status. Gen. Tech. Rep. PSW-133. Berkeley, CA: U.S. Department of Agriculture, Pacific Southwest Research Station: 225-246.

McNab, B.K. 1992. Energy expenditure: a short history. In: Thomasi, T.E.; Horton, T.H., eds. Mammalian energetics. Ithaca, NY. Comstock: 1-15.

Mead, R.A. 1994. Reproduction in *Martes.* In: Buskirk, S.W.; Harestad, A.; Raphael, M., comps. eds. Biology and conservation of martens, sables and fishers. Ithaca, NY. Cornell University Press: 404-422.

Moors, P.J. 1977. Studies of the metabolism, food consumption and assimilation efficiency of a small carnivore, the weasel (*Mustela nivalis*). Oecologia. 27:185-202.

Morrison, P.H. 1988. Old growth in the Pacific Northwest: a status report. Washington, DC: The Wilderness Society. 46 p.

Morse, W.B. 1961. Return of the fisher. American Forester. 64(4): 24-26, 47.

Obbard, M.E. 1987. Fur grading and pelt identification. In: Novak, M; Baker, J.A.; Obbard, M.E., comps., eds. Wild furbearer management and conservation in North America. North Bay, Ontario: Ontario Trappers Assocation: 1007-1033.

Olson, H.F. 1966. Return of a native. Wisconsin Conservation Bulletin. 31: 22-23.

Pack, J.C.; Cromer, J.I. 1981. Reintroduction of fisher in West Virginia. Worldwide Furbearer Conference Proceedings; Frostburg, Maryland. 2: 1431-1442.

Paragi, T.F. 1990. Reproductive biology of female fishers in southcentral Maine. Orono, ME: University of Maine. 107 p.

Parson, G.R. 1980. In: Douglas, C.W.; Strickland, M.A., eds. In: Transaction of 1979 Fisher Conference. Ontario Ministry of Natural Resources; [Unpubl. rep.]: 25-60.

Penrod, B. 1976. Fisher in New York. Conservationist. 31(2): 23.

Petersen, L.R.; Martin, M.A.; Pils, C.M. 1977. Status of fishers in Wisconsin, 1975. Madison, WI: Wisconsin Department of Natural Resources; Report No. 92.

Petskoi, P.G.; Kolpovskii, V.M. 1970. [Neck glandular structure in animals of the family Mustelidae]. Zool. Zhur. 49:1208-1219. In Russian.

Pittaway, R.J. 1978. Observations on the behaviour of the fisher (*Martes pennanti*) in Algonquin Park, Ontario. Le Naturaliste Canadienne. 105: 487-489.

Pittaway, R.J. 1984. Fisher, *Martes pennanti,* scent marking behaviour. Canadian Field-Naturalist. 98:57.

Powell, R.A. 1976. Compact carnivore. Animal Kingdom. 78(6):12-19.

Powell, R.A. 1977. Hunting behavior, ecological energetics and predator-prey community stability of the fisher (*Martes pennanti*). Chicago, IL: University of Chicago. Ph.D. thesis. 132 p.

Powell, R.A. 1978. A comparison of fisher and weasel hunting behavior. Carnivore. 1(1): 28-34.

Powell, R.A. 1979a. Mustelid spacing patterns: variations on a theme by Mustela. Z. Tierpsychol. 50: 153-165.

Powell, R.A. 1979b. Fishers, population models and trapping. Wildlife Society Bulletin. 7: 149-154.

Powell, R.A. 1980. Fisher arboreal activity. Canadian Field-Naturalist. 94: 90-91.

Powell, R.A. 1981a. *Martes pennanti.* Mammalian Species. 156:1-6.

Powell, R.A. 1981b. Hunting behavior and food requirements of the fisher (*Martes pennanti*) In: Chapman, J.A.; Pursley, D., eds. Proceedings of the 1st Worldwide Furbearer Conference; Baltimore, MD: Worldwide Furbearer Conference, Inc: 883-917.

Powell, R.A. 1985. Fisher pelt primeness. Wildlife Society Bulletin. 13: 67-70.

Powell, R.A. 1991. Thoughts on fishers and forests on the Olympic Peninsula. [Unpub. rep.] Portland, OR: U.S. Department of Agriculture, Pacific Northwest Research Station. 3 p. In cooperation with

Olympic National Park: U.S. Department of Interior, National Park Service.

Powell, R.A. 1993. The fisher: Life history, ecology and behavior. 2d ed. Minneapolis, MN: University of Minnesota Press. 237 p.

Powell, R.A. 1994a. Structure and spacing of *Martes* populations. In: Buskirk, S.W.; Harestad, A.; Raphael, M., comps. eds. Martens, sables and fishers: biology and conservation. Ithaca, NY: Cornell University Press: 101-121.

Powell, R.A. 1994b. Scale and habitat selection by fishers in Upper Peninsula Michigan in winter. Journal of Mammalogy. 75: 349-356.

Powell, R.A.; Brander, R.B. 1977. Adaptations of fishers and porcupines to their predator-prey system. In: Phillips, R.L.; Jonkel, C., eds. Proceedings of 1975 Predator Symposium; Montana Forest Conservation Experiment Station; Missoula, MT. Missoula, MT: University of Montana: 45-53.

Powell, R.A.; Zielinski, W.J. 1983. Competition and coexistence in mustelid communities. Acta Zoologica Fennica. 174: 223-227.

Pringle, L. 1964. Killer with a future-the fisher. Animal Kingdom. 67:82-87.

Proulx, G.; Kolenosky, A.; Badry, M. [et al.]. 1994. Post-release movements of translocated fishers. In: Buskirk, S.W.; Harestad, A.; Raphael, M., comps. eds. Martens, sables and fishers: biology and conservation. Ithaca, NY: Cornell University Press: 197-203.

Quick, H.F. 1953. Wolverine, fisher and marten studies in a wilderness region. In: Transactions of the North American Wildlife Conference. 18: 513-533.

Rahel, F.J. 1990. The hierarchical nature of community persistence: A problem of scale. American Naturalist. 136: 328-344.

Raine, R.M. 1979. Ranges of juvenile fisher, *Martes pennanti,* and marten, *Martes americana,* in southeastern Manitoba. Canadian Field-Naturalist. 96: 431-438.

Raine, R.M. 1983. Winter habitat use and responses to snow of fisher (*Martes pennanti*) and marten (*Martes americana*) in southeastern Manitoba. Canadian Journal of Zoology. 61: 25-34.

Raine, R.M. 1987. Winter food habits and foraging behaviour of fishers (*Martes pennanti*) and martens (*Martes americana*) in southeastern Manitoba. Canadian Journal of Zoology. 65: 745-747.

Rand, A.L. 1944. The status of the fisher (*Martes pennanti* Erxleben) in Canada. Canadian Field-Naturalist. 58: 77-81.

Raphael, M.G. 1984. Wildlife populations in relation to stand age and area in Douglas-fir forests of northwestern California. In: Meehan, W R.; Merrell, T.R., Jr.; Hanley, T.A., eds. Fish and Wildlife relationships in old-growth forests. American Institute of Fisheries Research Biologists: 259-274.

Raphael, M.G. 1988. Long-term trends in abundance of amphibians, reptiles, and mammals in Douglas-fir forests of northwestern California. In: Szare, R.C.; Severson, K.E.; Patton, D.R., eds. Management of amphibians, reptiles, and small mammals in North American. Gen. Tech. Rep. RM-166. Fort Collins, CO: U.S. Department of Agriculture, Rocky Mountain Forest and Range Experiment Station: 23-31.

Reynolds, J.; Self, S. 1994. Martens and fishers: habitat use in managed forests, a review. Redding, CA: Sierra Pacific Industries; [Unpubl. rep.]. 10 p.

Rosenberg, K.V.; Raphael, R.G. 1986. Effects of forest fragmentation on vertebrates in Douglas-fir forests. In: Verner, J.; Morrison, M.L.; Ralph, C.J., eds. Wildlife 2000: Modeling habitat relationships of terrestrial vertebrates. Madison, WI: University of Wisconsin Press: 263-272.

Rosenzweig, M.L. 1966. Community structure in sympatric Carnivora. Journal of Mammalogy. 47: 602-612.

Roy, K.D. 1991. Ecology of reintroduced fishers in the Cabinet Mountains of northwest Montana. Missoula, MT: University of Montana M.S. thesis. 94 p.

Roze, U. 1989. The North American porcupine. Washington, DC: Smithsonian Institution Press. 261 p.

Roze, U.; Locke, D.C.; Vatakis, N. 1990. Antibiotic properties of porcupine quills. Journal of Chemical Ecology. 16: 725-734.

Rozhnov, V.V. 1991. Changes in the marking behavior in marten evolution. In: Powell, R.A.; Buskirk, S.W., comps., eds. Abstracts of presentations: Symposium on the biology and management of martens and fishers; 1991 May 29-June 1; Laramie, WY Laramie, WY. University of Wyoming: 71.

Ruggiero, L.F.; Aubry, K.B.; Carey, A.B. [et al.]. 1991. Wildlife and vegetation of unmanaged Douglas-fir forests. Gen. Tech. Rep. PNW-285. Portland, OR: U.S. Department of Agriculture, Pacific Northwest Research Station. 533 p.

Sandell, M. 1986. Movement patterns of male stoats, *Mustela erminea,* during the mating season: Differences in relation to social status. Oikos. 47: 63-70.

Sandell. M. 1989. The mating tactics and spacing pat-

terns of solitary carnivores. In: Gittleman, J.L., ed. Carnivore behavior, ecology, and evolution. Ithaca, NY: Cornell University Press: 164-182.

Scheffer, V.B. 1949. Mammals of the Olympic Peninsula, Washington. [Unpubl. Rep. to U. S. Department of Interior, Fish and Wildlife Service]. On file at Port Angeles, WA: U.S. Department of Interior, Olympic National Park. 248 p.

Schempf, P.F.; White, M. 1977. Status of six furbearers in the mountains of northern San Francisco, CA: U.S. Department of Agriculture, Forest Service, Pacific Southwest Region. 51 p.

Schmidt, K.N.; Schmidt, G.A.; Zielinski, W.J. 1993. Pilot Creek carnivore study, Six Rivers National Forest. Progress Report. [Unpubl. rep.]. Berkeley, CA: U.S. Department of Agriculture, Forest Service, Six Rivers National Forest and Pacific Southwest Research Station. 4 p.

Schorger, A.W. 1942. Extinct and endangered mammals and birds of the Great Lakes Region. In: Transactions of Wisconsin Academy of Science; Arts and Letters. 34: 24-57.

Scott, T.G. 1941. Methods and computation in fecal analysis with reference to the red fox. Iowa State College Journal of Science. 15: 279-285.

Scott, W.E. 1939. Rare and extinct mammals of Wisconsin. Wisconsin Conservation Bulletin. 4(10): 21-28.

Seaman, D.E. 1993. Home range and male reproductive optimization in black bears (*Ursus americanus*). Raleigh, NC: North Carolina State University. Ph.D. thesis.

Seglund, A.; Golightly, R.T., Jr. 1994. Fisher survey techniques on the Shasta-Trinity National Forest. Arcata, CA: Humboldt State University; Progress Report. [Unpub. rep.]. 14 p. In cooperation with the U.S. Department of Agriculture, Forest Service.

Self, S.E.; Kerns, S.J. 1992. Pine marten-Pacific fisher study, phase II report, 10 June 1992. Redding, CA: Wildland Resource Managers; [Unpub. rep.]. 34 p.

Shaffer, M.L. 1981. Minimum population sizes for species conservation. Bioscience. 31: 131-134.

Shea, M.E.; Rollins, N.L.; Bowyer, R.T.; [et al.] 1985. Corpora lutea number as related to fisher age and distribution in Maine. Journal of Wildlife Management. 49: 37-40.

Silver, H. 1957. A history of New Hampshire game and furbearers. Concord, NH: New Hampshire Fish and Game Department.

Silverman, B.W. 1990. Density estimation for statistics and data analysis. London: Chapman and Hall, Ltd. 175 p.

Sokolov, I.I.; Sokolov, A.S. 1971. [Some characteristics of locomotor organs of *Martes martes* L. associated with its mode of life.]. Byull. Mosk. O-va. Ispt. Priv. Otd. Biol. 76(6): 40-51.

Stevens, C.L. 1968. The food of fisher in New Hampshire. Concord, NH: New Hampshire Department of Fish & Game; [Unpubl. rep.].

Strickland, M.A. 1994. Harvest management of fishers and American martens. In: Buskirk, S.W.; Harestad, A.; Raphael, M., comps. eds. Martens, sables and fishers: biology and conservation. Ithaca, NY: Cornell University Press: 149-164.

Strickland, M.A.; Douglas, C.W. 1978. Some predictions for fisher and marten harvests in, 1978-1979. Canadian Trapper. (December): 18-19.

Strickland, M.A.; Novak, M.; Hunzinger, N.P. 1982. Fisher. In: Chapman, J.A.; Feldhamer, G.A., eds. Wild mammals of North America: biology, management, and economics. Baltimore, MD: Johns Hopkins University Press: 586-598.

Tapper, S.C. 1976. The diet of weasels, *Mustela nivalis,* and stoats, *Mustela erminea,* during early summer, in relation to predation on gamebirds. Journal of Zoology. 179: 219-224.

Tapper, S.C. 1979. The effect of fluctuating vole numbers (*Microtus agrestis*) on a population of weasels (*Mustela nivalis*) on farmland. Journal of Animal Ecology. 48: 603-617.

Thomas, J.W; Raphael, M.G.; Anthony, R.G. [et al.]. 1993. Viability assessments and management considerations for species associated with late-successional and old-growth forests of the Pacific Northwest. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Region. 523 p.

Thomasma, L.E.; Drummer, T.; Peterson, R.O. 1991. Testing the habitat suitability index model for the fisher. Wildlife Soceity Bulletin. 19: 291-297.

Thomasma, L.E.; Drummer, T.; Peterson, R.O. 1994. Modeling habitat selection by the fisher. In: Buskirk, S.W.; Harestad, A.; Raphael, M., comps. eds. Martens, sables and fishers: biology and conservation. Ithaca, NY: Cornell University Press: 316-325.

U.S. Department of Agriculture. 1994. Final Supplemental Environmental Impact Statement on Management of Habitat for Late-Successional and Old-Growth Forest Related Species within the Range of the Northern Spotted Owl. Portland, OR: U.S. Department of Agriculture, Forest Service. In cooperation with U.S. Department of Interior, Bureau of Land Mangement.

U.S. Department of Interior, Fish and Wildlife Service. 1991. Notice of petition finding: 90-day petition finding for the Pacific fisher. Federal Register. 58:1159-1161.

Weckwerth, R.P.; Wright, P.L. 1966. Results of transplanting fishers in Montana. Journal of Wildlife Management. 32: 977-980.

Weckwerth, R.P.; Wright, P.L. 1968. Results of transplanting fishers in Montana. Journal of Wildlife Management. 32: 977-980.

Whitaker, J.O., Jr. 1970. The biological subspecies: An adjunct of the biological species. The Biologist. 52: 11-15.

Williams, R.M. 1962. The fisher returns to Idaho. Idaho Wildlife Reveiw. 15(1): 8-9.

Wilson, D.S. 1975. The adequacy of size as a niche difference. American Naturalist. 109: 769-784.

Wood, J. 1977. The fisher is: . . .. National Wildlife. 15(3):18-21.

Worthen, G.L.; Kilgore, D.L. 1981. Metabolic rate of pine marten in relation to air temperature. Journal of Mammalogy. 62: 624-628.

Wright, P.L.; Coulter, M.W. 1967. Reproduction and growth in Maine fishers. Journal of Wildlife Management. 31: 70-87.

Yocum, C.E; McCollum, M.T. 1973. Status of the fisher in northern California, Oregon and Washington. California Fish and Game. 59(4): 305-309.

York, E.C.; Fuller, T.K. [In press]. Fisher population dynamics: in pursuit of lambda. International Union Game Biologists.

Young, H.C. 1975. Pequam the fisher. Fur-Fish-Game. 71(11):16-17,48-50.

Zielinski, W.J. 1986. Relating marten scat contents to prey consumed. California Fish and Game. 72: 110-116.